Institut für Landschaftsökologie und Ressourcenmanagement
-Professur für Landschaftsökologie und Landschaftsplanung-

Restoration of alluvial grasslands: Effects of flooding and management on plant dispersal and recruitment

Dissertation zur Erlangung des Doktorgrades
(Dr. agr.)
am Fachbereich Agrarwissenschaften, Ökotrophologie und Umweltmanagement
der Justus-Liebig Universität Gießen

eingereicht von
Dipl. Biol. Stephanie Bissels

Gießen 2005

Dekan: Prof. Dr. Wolfgang Köhler

1. Gutachter: Prof. Dr. Dr. Annette Otte
2. Gutachter: Prof. Dr. Gerd Esser

This thesis is based on the following four papers:

I. Bissels, S., Hölzel, N., Donath, T.W. & Otte, A. 2004. Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biological Conservation* 118: 641-650.

II. Bissels, S., Donath, T.W., Hölzel, N. & Otte, A. Ephemeral wetland vegetation in irregularly flooded arable fields along the northern Upper Rhine: the importance of persistent seed banks. *Phytocoenologia* (in press).

III. Bissels, S., Donath, T.W., Hölzel, N. & Otte, A. Effects of different mowing regimes and environmental variation on seedling recruitment in alluvial grasslands. (submitted).

IV. Bissels, S., Hölzel, N. & Otte, A. 2004. Population structure of the threatened perennial *Serratula tinctoria* in relation to vegetation and management. *Applied Vegetation Science* 7: 267-274.

In the first paper I performed a part of the field work and had the main responsibility for data analysis and writing. The co-authors were involved in planning the study, contributed to field work and gave valuable comments.
In paper II the first two authors contributed equally to the development of the paper. They planned the study, did the field work as well as data analysis and writing. The co-authors provided helpful ideas and criticism.
In paper III and paper IV I had the main responsibility for field work, data analysis and writing while the co-authors were involved in study design and contributed constructive suggestions and helpful comments.

Table of Contents

1 General introduction

1.1 Background

In many Central European semi-natural grasslands changes in agricultural management led to changes in floristic composition and usually to a loss in species-richness. These changes have not only been caused by intensification of management such as fertilizer application, frequent mowing or drainage but also by abandonment. Consequently, many formerly common types of semi-natural grasslands have become extinct or fragmented. In particular flood-plain grasslands such as *Cnidion*- and alluvial *Molinion*-meadows are currently among the most endangered plant communities in Central Europe (Korneck et al. 1996; Joyce & Wade 1998, Schnittler & Günther 1999). The distribution of subcontinental alluvial grasslands of the *Cnidion* alliance in Central Europe is strongly confined to large lowland rivers with warm and dry subcontinental climate and many rare and characteristic species reach the north-western limits of their distribution area at the river Rhine (Hultén & Fries 1986). Ecologically, these meadows are characterized by a high variability in soil water potential including inundation periods in winter, spring and early summer as well as regular periods of severe summer drought. This leads to a quite distinct species composition: Besides species of mesic habitats, species with a high flooding tolerance as well as those adapted to dry conditions may be found in these meadows. In addition to the limited distribution and specific habitat requirements of flood-meadow species, intensified agricultural management and alterations of natural hydrological conditions are further reasons for their decline and the need of priority conservation measures for this grassland type.

Along the northern Upper Rhine intensified drainage, structural changes in agriculture and the conversion of alluvial grasslands into arable fields until the late 1980s resulted in a significant decline of characteristic flood-meadow species. Consequently, the target species are now restricted in a few non-intensively managed meadows within nature reserves or small remnants along a system of drainage ditches and other linear structures (Donath et al. 2003). Since this situation is typical of many large rivers in Central Europe, such as Elbe, Oder or Danube, the restoration of these rare flood-plain communities is a growing concern of biodiversity conservation (Burkart 2001; Hölzel & Otte 2003).

For restoration purposes it is essential to sample ecological background knowledge and to identify factors that enhance or hamper restoration success. Abiotic site conditions, particularly high levels of fertilizer residuals after cessation of agricultural use have been identified as obstacles to re-establishment of semi-natural grasslands (Kapfer 1988; Gough &

Marrs 1990; Oomes 1990). However, in many recent restoration projects lowering the soil nutrient status and biomass production or simply installing the former management practices did often not result in the desired species-enrichment (Bakker 1989; Bakker & Berendse 1999). Moreover, recent studies have revealed that biotic constraints are also of high importance. Soil seed banks as a potential for re-colonisation are usually impoverished after years of intensive agricultural management and many target species are not capable of forming a persistent seedbank (Bekker et al. 1997; Thompson et al. 1997). Therefore, restoration of target communities largely depends on highly stochastic processes like dispersal and recruitment. Target species mostly have to immigrate from the near vicinity of restoration sites, which is often restricted by the lack of source populations in the increasingly fragmented cultural landscape (Donath et al. 2003). Additionally, traditional dispersal vectors such as grazing livestock (Fischer et al. 1996), hay making or sowing of hay residuals (Bonn & Poschlod 1998) are largely ceased in the modern agricultural landscape.

Due to the fact that dispersal is often considered to be the bottleneck in restoration it is of high importance to improve our knowledge about dispersal and colonization processes of endangered plant species with respect to their specific habitat conditions. Particularly with regard to highly endangered flood-meadow species information about population biology and population dynamics is currently scarce (Burkart 2001).

Seed Dispersal

A large variety of dispersal types exist among plant species. The most important mechanisms are dispersal by animals, wind, or water. However, our knowledge about dispersal properties of grassland species and their dispersal distances is very limited (Bakker et al. 1996). Most seeds end up relatively close to the parent plant, but rare long-distance dispersal events also occur and may be particularly important for restoration purposes (Cain et al. 2000).

Beside dispersal in space, seeds can also be dispersed in time which means the incorporation into a soil seedbank (Grubb 1977; Bakker et al.1996; Grime 2002). Since seeds of different species vary in their longevity in the seedbank, some seeds remain dormant in the soil for many years. However, persistent seedbanks mainly contain pioneer species and weeds while most grassland species have short-lived seeds (Bekker at al. 1997). Therefore, in grasslands, re-establishment from source populations or from vegetative propagation play a dominant role.

In alluvial meadows, seed dispersal by river water entering the flood-plain is often regarded as a significant dispersal vector (Bakker et al. 1996; Johansson et al. 1996; Bonn & Poschlod

1998) and it is assumed that the restoration of natural hydrological conditions is a prerequisite facilitating diaspore input during high floods (Tockner et al. 2000). Many species are recorded in litter material of drift lines created by flooding in relatively natural flood-plains (Skoglund 1990; Andersson et al. 2000) or on sedimentation mats in nearby meadows (Vogt et al. 2004). However the significance of flood dispersal for restoration is controversially discussed and not yet understood. Studies along the northern Upper Rhine or along other largely confined rivers showed that flooding events did not raise the input of diaspores in the seedbank (Hölzel & Otte 2001) and was even ineffective in dispersing species in the proximity of source populations (Bischoff 2002).

Seedling recruitment

Seed germination and seedling establishment are crucial stages in the life cycle of plant species. Besides the availability of seeds, the lack of suitable microsites is identified as another limiting factor in seedling recruitment. Seedling recruitment requires specific conditions which may differ considerably from those of established plants (Grubb 1977). Emerging seedlings are much more sensitive towards unfavourable physical conditions such as frost and drought (Ryser1993) as well as competition by established plants (Rusch & Fernandéz-Palacios 1995; Kotorová & Lepš 1999). In particular in closed grassland swards, gaps are of high importance for successful seedling recruitment (Grime 2002, Goldberg 1987) and for many small-seeded grassland species a dependence on gaps could be confirmed (Gross 1984). However, the importance of gap regeneration may differ considerably among species (Fenner 1978) and among the studied sites or years.

External factors are crucial not only for creating gaps in the plant community but also for determining which species will successfully establish in gaps. This means that external factors may also influence seed production, dispersal and recruitment of plant species. Management practices, for example, regular mowing or grazing are known to provide gaps in the sward that enhance seedling establishment (Bakker et al. 1980; Watt & Gibson 1988; Hutchings & Booth 1996; Kotorová & Lepš 1999). Moreover the number of available seeds may also be reduced by land use, for example by early mowing (Coulson et al. 2001) or dispersal may be affected by sheep grazing (Fischer et al. 1996).

In wetlands, flooding can be seen as another factor influencing seedling recruitment. Flooding also creates gaps in the vegetation and prevents competitive exclusion (Bornette & Amoros 1996). However, due to anaerobic stress, long lasting inundation periods may also negatively

influence survival and growth of seedlings (van den Brink et al. 1995; Blom & Voesenek 1996).

1.2 Objectives

The general aim of this study was to identify and assess the relative importance of factors limiting the successful restoration of flood-plain communities.

The study is at first based on the evaluation of large-scaled restoration measures of alluvial meadows on former arable fields along the northern Upper Rhine. Starting in the 1980s, 300 ha of arable land were converted into grassland by natural regeneration but also by sowing of a species-poor mixture of common grasses (Dister et al 1992). Subsequently the meadows were managed extensively, i.e. mown once from June onwards without application of fertilizer. However, as experienced in many other restoration projects (Bakker & Berendse 1999) even after 20 years the restoration measures did not result in the desired species-enrichment (Hölzel et al. 2002; Donath et al. 2003). Adverse abiotic site conditions and raised nutrient levels in particular, are often regarded as a major obstacle to the restoration of species-rich communities (Kapfer 1988; Oomes 1990; Marrs 1993). Thus, the relative importance of soil nutrient status and productivity on species composition was analysed in a comparative study. Furthermore, limited seed dispersal of target species could potentially be a main cause for the failure of restoration attempts in the study area (Bischoff 2002, Donath et al. 2003). In our case, a particularly high significance of fluvial transport was assumed (Dister et al. 1992). Seed dispersal by river water is generally regarded as a very effective dispersal vector in flood-plains (Bakker et al. 1996; Johansson et al. 1996; Bonn & Poschlod 1998) and the reconnection of dyked areas to the natural flooding regime is thought to be a prerequisite for the restoration of species-richness (Tockner et al. 2000).Therefore it was investigated if there is really a significant impact of flood dispersal on species-enrichment in our concrete example of a strongly confined large lowland river such as the Rhine. Knowledge on seed longevity is essential to assess the role of persistent soil seed banks in restoration (Bekker et al. 1997; Thompson et al. 1997; Hözel & Otte 2004b) Therefore we studied the soil seedbanks of arable fields to see if they contain seeds of target species that may contribute to the restoration of alluvial grasslands. The lack of suitable microsites in dense species-poor grassland swards (Kotorová & Lepš 1999) is another potential constraint for the establishment of desired target species in restoration. Therefore we tried to clarify the role of different mowing regimes on recruitment success. Finally, the important issue how different types of

grassland management affect the population viability and persistence of target species (Bakker et al. 1980; Watt & Gibson 1988; Coulson et al. 2001) was investigated. This was done by analysing the population stage structure of the model species *Serratula tinctoria* in relation to environmental conditions and under different management regimes, which were applied by conservation authorities and farmers in the region. Such studies are of high practical relevance to assess perspectives for the incorporation of grassland management in farming systems (Donath et al 2004).

After a short introduction to the study area (chapter 2) and an overview of data collection and statistical analyses (chapter 3) the four following chapters comprise detailed studies, which will be separately introduced:

Evaluation of restoration success (chapter 4)

Questions: To what extent did target species and communities re-establish? Which are the constraints that hamper restoration success? Is the goal of restoration enhanced or hampered by direct flooding with river water?

In chapter 4 large-scaled restoration measures aiming at the re-establishment of species-rich alluvial grasslands along the northern Upper Rhine are evaluated. Floristic composition, soil nutrient status and biomass production of newly created meadows were compared with existing species-rich old meadows with respect to different flooding regimes. Whereas the recent functional flood-plain is exposed to direct flooding, the fossil flood-plain is protected by a dyke and only submerged by ascending groundwater. Thus, in the latter compartment the input of diaspores by river water is precluded. We examined whether species composition is limited preliminary by abiotic site conditions or by other biotic constraints, e.g. the ability to reach suitable habitats. It was hypothesised that restoration in terms of species-enrichment will be more successful in the functional flood-plain due to the input of propagules in the course of flooding events.

Soil seedbanks of irregularly flooded arable fields (chapter 5)

Questions: Do target species of alluvial grasslands occur in the soil seedbank of arable fields? How is the composition and size of the seedbank related to above-ground vegetation, water regime and management? Are temporarily flooded arable fields a significant habitat for ephemeral wetland vegetation?

A further focus was on the significance of the seedbank for the restoration of alluvial grasslands on former arable fields. We assessed the composition and the size of the soil

seedbank of irregularly flooded arable fields with respect to the ephemeral wetland vegetation, which had developed after a long-lasting spring and early summer flood in 2001. Based on this data, the relation of the seedbank to above-ground vegetation, water regime and management was investigated. Furthermore, we compared our vegetation data with other phytosociological studies of mudflat communities from primary and secondary habitats.

Seedling recruitment in alluvial grasslands (chapter 6)

Questions: Is target species-enrichment in the studied alluvial grasslands limited by microsite availability? Which effects did mowing show on seedling recruitment? Did other factors such as flooding regime, vegetation structure or environmental variation influence seedling recruitment?

To overcome dispersal limitation in the fragmented landscape as well as the lack of target species in the soil seedbank of alluvial grasslands, sowing of seeds may enhance restoration success. But even if seeds of target species are added the availability of suitable microsites for seedling recruitment is another constraint to successful re-establishment. Grassland management by grazing and/or cutting has been shown to be a very important factor determining recruitment success. Thus, in chapter six we studied the effects of different management regimes and environmental variation on recruitment in dense species-poor grassland swards. We conducted seed addition experiments with six typical flood-meadow herbs in two alluvial grasslands with different flooding regimes and assessed the impact of mowing and other factors such as flooding regime, vegetation structure and environmental variation on seedling recruitment.

Population structure of *Serratula tinctoria* (chapter 7)

Questions: How does vegetation and management affect the population stage structure of *Serratula tinctoria*, a species indicative of highly endangered flood-plain meadows? Are different management regimes suitable to support viable populations of *S. tinctoria?*

The evaluation of management schemes is of high practical relevance for a successful restoration and maintenance of endangered semi-natural grassland communities. In this context the viability of target species populations may serve as a particularly useful indicator. We studied the stage structure of 24 populations of the threatened perennial *Serratula tinctoria* with respect to vegetation, site conditions and management. The main objective was to evaluate management options for the sustainable conservation of *S. tinctoria* populations and species-rich flood-meadows in general. For restoration purposes this is also of high

significance since local survival of remaining autochthonous populations that may function as source populations in conservation programs often depends on an appropriate management. The results may also provide useful information about how different management regimes affect populations of flood-meadow species on newly created restoration sites.

The results of the previous chapters are summarized and discussed in a general discussion (chapter 8.1). Finally, an outline for future research is given (chapter 8.2).

2 Study area

The study area is situated in the Hessian part of the Holocene flood-plain along the northern Upper Rhine between the tributaries Neckar to the south and Main to the north (Fig. 1). While most of the studies (chapter 4, 5, 6) were conducted within and in the closer surroundings of the nature reserves 'Kühkopf-Knoblochsaue' and 'Riedwiesen von Wächterstadt,' about 30 km southwest of Frankfurt (Fig. 2), for the study in chapter 7 meadows spread over the whole study area were selected (Fig.1). The two above mentioned nature reserves are located in the municipality of Riedstadt and contain approximately 450 ha of old species-rich flood-meadows and 300 ha of restoration grassland on ex-arable land. Furthermore, the meadows selected within the study area differ with respect to their flooding regime. While the functional flood-plain is exposed to direct flooding of up to 3 m above terrain, the fossil flood-plain is protected by dykes and only submerged in low depressions (< 1m) by ascending ground-water (Fig. 2).

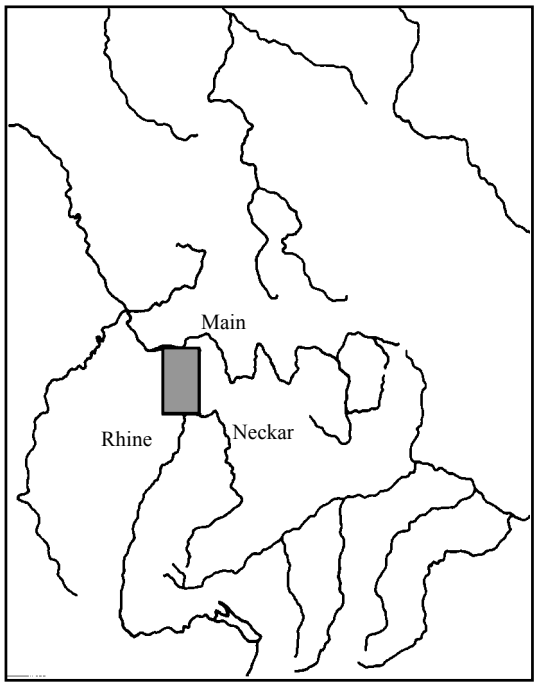

Fig. 1. Map of the main rivers in Germany and geographical location of the study area (grey box) (c.f. Böger 1991).

The meadows of the studied type occupy fine-grained, calcareous alluvial soils which are irregularly flooded during high water levels of the Rhine. In conjunction with the warm and dry climate in the region, with a mean annual precipitation of 580 mm and a mean annual temperature of 10.3°C (Müller-Westermeier 1990), this leads to a high variability in soil water potential. While winter, spring and early summer may bring floods, summers are remarkably dry. Additionally, due to the high clay content (> 60%) plant available water is rapidly declining shortly after the retreat of water.

Species composition of the old meadows that reflect the target community, is commonly referred to as *Allium angulosum* - *Alopecurus pratensis* - flood meadow (alliance *Cnidion*) with an average duration of flooding between 8 and 25 days per year, while higher elevations with short-term flooding are occupied by the mesic alluvial *Arrhenatherion*-meadow (Hölzel 1999). The *Cnidion*-meadow contain a large number of rare and endangered species of predominantly subcontinental distribution, which are confined to large river corridors and

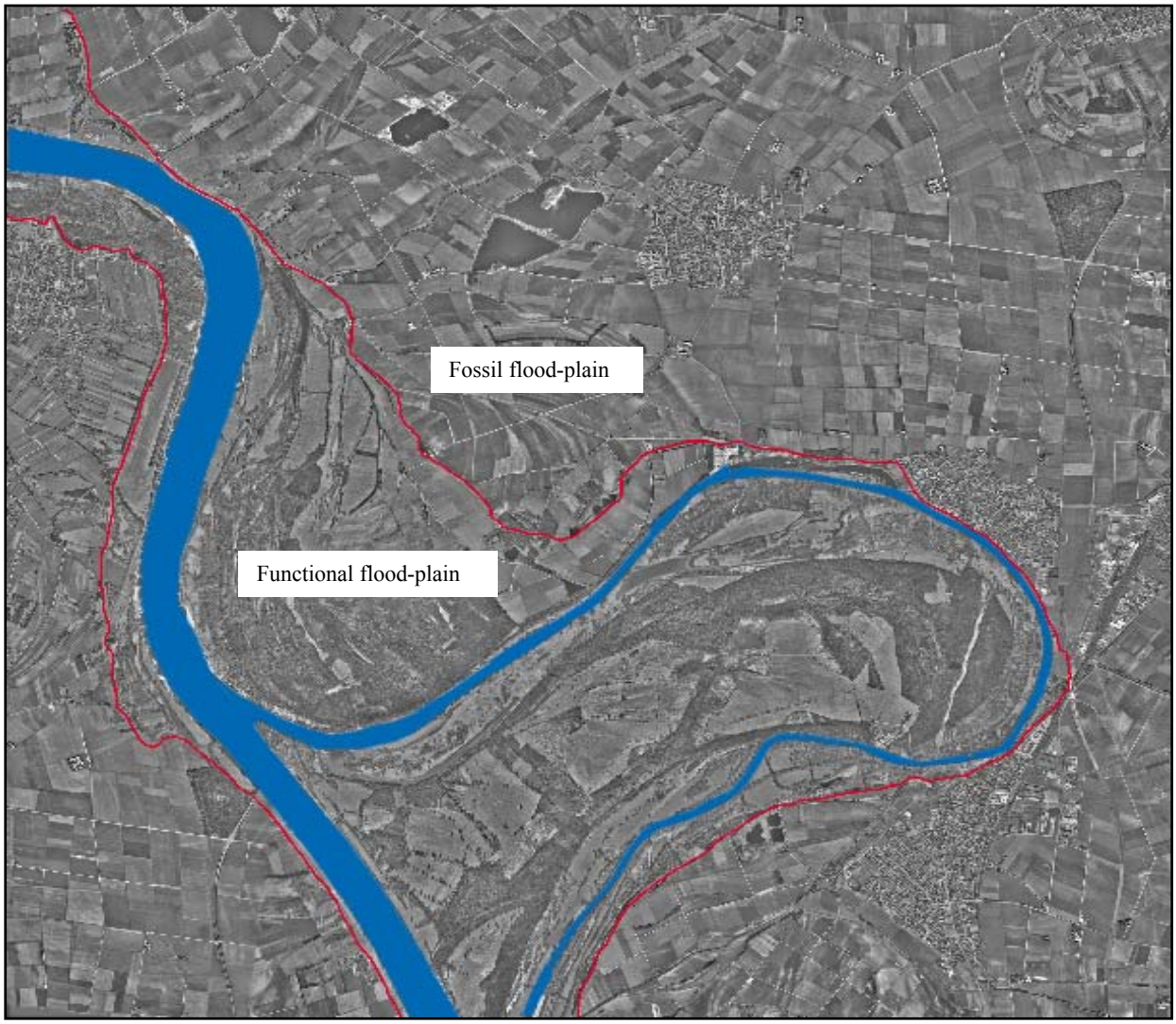

Fig. 2. Functional and fossil flood-plain in the study area. The functional flood-plain comprises the land between the river and the high winter dykes (red line) whereas the fossil flood-plain is located on the landward site of the winter dykes.

partly reach the western boundary of their areal along the northern Upper Rhine (e.g. *Allium angulosum, Cnidium dubium* or *Viola pumila)* (Hultén & Fries 1986).

Until the 1950s (Knapp 1954) and even 1960s, species-rich alluvial grasslands that were managed extensively as hay-meadows dominated the whole area (shown in Fig. 2). Intensified drainage (since the 1920s) across the whole area, structural changes in agriculture (Lambrecht 1983) and a series of dry years during the 1970s and 1980s accelerated the conversion into arable fields even in the lowest part of the area (Böger 1991). Starting in 1983 (functional flood-plain) and 1988 (fossil flood-plain), about 300 ha of arable land were converted into grassland. This was done mostly by natural regeneration but partly also by sowing with species-poor mixtures of common grasses or with freshly threshed material from species-poor, grass-dominated meadows. After the creation of a closed sward the meadows were

managed extensively, i.e. mown from June onwards without application of fertilizer. Sometimes the meadows are additionally grazed by sheep or mown for a second time in September or October. These management practices were also applied to existing alluvial grasslands in the study area.

Due to favourable edaphic and climatic conditions as well as drainage, intensive agricultural production (e.g. cereals, maize and sugar beats) is still common and profitable in the fossil flood-plain. However, the large-scaled nature conservation measures carried out in the 1980s and further restoration attempts in the fossil flood-plain which started in 2000 reduced the amount of arable fields and led to an increase of alluvial grasslands.

More detailed information with focus on the different research topics will be found in the material and methods or study area sections of the chapters 4, 5, 6 and 7.

3 Data collection and statistical analyses

Here the sampling methods and the methods of data analysis used in the thesis are summarized. In general, we differentiate between comparative or correlative studies (chapter 4, 5 and 7) and experiments (chapter 6). Several methods of both exploratory data analysis, e.g. ordination or cluster analysis, and inferential statistics, i.e. methods that allow statistical hypotheses testing, such as regression analysis and analysis of variance (Jongman et al. 1995), were applied in the thesis. In analysis of complex data sets like plant community data, these two approaches are often combined. Therefore in chapter 3.1 exploratory studies which are combined with other formal statistical analyses, are summarized (chapter 4, 5 and 7). In chapter 3.2 a manipulative, factorial experiment, where the null hypothesis was clearly stated before the experiment started, is introduced (chapter 6).

3.1 Exploratory data analysis

Sampling of vegetation and other habitat variables

Different methods for sampling of vegetation and other habitat variables were applied. To describe species composition in the study of evaluation of restoration success (chapter 4), the abundance of all vascular plant species was estimated on 10 x 10 m plots using a modified Braun-Blanquet scale (van der Maarel 1979). For the study of ephemeral wetland vegetation 5 x 5 m plots were sampled (chapter 5). To determine dry matter yield of biomass, ten randomly distributed quadrats of 0.1 m² area were cut near the soil surface, dried and weighed (chapter 4). For the investigation of the population structure of *Serratula tinctoria* (chapter 7), several indicators of vegetation structure were estimated: Total vegetation cover, the coverage of mosses, plant litter, the percentage of bare soil surface and the mean vegetation height. Moreover, light measurements were undertaken in two studies (chapter 6 and 7). Using a Line Quantum Sensor of one meter length (LI-COR: LI-191SA) light intensity penetrating to the ground was recorded. Photosynthetically active radiation (PAR, 400-700 nm) was measured simultaneously at ground level and in full light above the canopy. Light penetration was expressed as a percentage of the latter value.

Soil nutrient analyses

For the evaluation of restoration success in chapter 4 we collected soil samples and conducted soil nutrient analyses. Plant available phosphorus and potassium were determined using the

Calcium-Acetate-Lactate extraction method (CAL) as described by Hoffmann (1991). Total nitrogen and total carbon were assessed using a CN-analyser (FlashEA 1112, Thermoquest). The $CaCO_3$ content of the soil was measured according to the method of Scheibler (Hoffmann 1991). This was done to calculate the organic matter content of the soil samples and the C/N-ratio, which was used as a measure of nitrogen availability (Kuntze et al. 1994).

Seed bank analyses

For the investigation of the soil seedbanks of irregularly flooded arable fields (chapter 5), soil seed samples were collected at each site by random collection of 20 cores of 10 cm depth. We analysed seedbanks using the seedling emergence method over 30 months (Roberts 1981; Hölzel & Otte 2001). After removing vegetative plant material the soil samples were transferred to Styrofoam trays and exposed under free air conditions. The trays were protected against diaspore input and heating by covering them with flat, white gauze lids. Control basins filled with sterile soil were placed between the samples. Germinating seedlings were identified and removed once every week.

To estimate the size of the seedbank of common agrestal species and ephemeral wetland vegetation, we exposed the samples to different water regimes. For the first 18 month the samples were exposed to terrestrial conditions with no flooding but regular watering. Prior to the third season of the study the samples were first shallowly flooded for three months and subsequently kept under waterlogged conditions.

Assessment of population biological parameters

In chapter 7 the population stage structure of the threatened perennial *Serratula tinctoria* is investigated and analysed. For this purpose 24 meadows with the model species *S. tinctoria* were chosen. In each of the 24 populations two 1 m² plots were randomly selected and the total number of individuals in each plot was counted. To classify the life stage classes the following parameters were measured: Total height of each individual, total length of the longest leaf, length and width of the longest leaf blade. Additionally, the number of leaves per rosette of each individual plant were counted. In generative plants the number of flowerheads and stalks was also recorded. To determine population size in small populations all flowering plants were counted. In large population (>500 individuals) the mean number of reproductive plants per m² was used and extrapolated to a value for the total population area.

Methods of data analysis

Classical phytosociological analyses of vegetation data have been used in chapter 5 (seedbanks of irregularly flooded arable fields) for the comparison of ephemeral wetland vegetation from primary and secondary habitats. The phytosociological classification of the species followed Oberdorfer (1983, 1992).

Generally a variety of methods of multivariate analysis of ecological data were conducted:

- Detrendend Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples. This ordination type was used in the study of evaluation of restoration success (chapter 4), the investigation of ephemeral wetland vegetation on arable fields (chapter 5) and the study of the population structure of *Serratula tinctoria* (chapter 7).
- Partial Redundancy Analysis (RDA) performed a decomposition of variance and was used to isolate the effect of moisture on vegetation composition in the study of the evaluation of restoration success (chapter 4).
- Indicator Species Analysis (Dufrene & Legendre 1997) was applied to identify significant indicators of old and new meadows for the evaluation of restoration success (chapter 4).
- K-means clustering was conducted to evaluate the appropriateness of the chosen classification and to clarify critical cases of life stage classes of *Serratula tinctoria* (chapter 7).
- The Mantel test (Legendre & Legendre 1998) was used to evalute the similarity between the soil seedbank and the established ephemeral wetland vegetation and to test for spatial proximity in the vegetation and seed bank (chapter 5).

Further statistical methods that were applied are:

- Simple and multiple regression analysis (GRM module in Statistica),
- Correlation analysis (Pearson and Spearman),
- Non-parametric Mann-Whitney U-test,
- One and two-way analysis of variance (ANOVA), nested ANOVA,
- Multivariate analysis of variance (MANOVA).

3.2 Factorial experiment

To asses the impact of mowing on seedling recruitment a seed addition experiment was carried out at two different sites (chapter 6). This experiment employed a split-plot design

with four replicate blocks. Within each main plot, six subplots of 30 x 30 cm were established and 100 seeds of one of six flood-meadow species were sown into each subplots. Mowing of plots was carried out with a cutter bar mower at different dates to establish three different mowing regimes.
The total number of seedlings in each plot was recorded in early summer, midsummer and autumn over two subsequent years.

Data analysis
To test for differences in treatments and species, repeated measures analyses (ANOVA and MANOVA) for a split-plot design were applied.
The following computer programs were used for statistical data analysis in this thesis: CANOCO (Ter Braak & Smilauer 1998), STATISTICA 5.1 and 6.0 (Anon. 1998, Anon. 2002), PC-Ord 4.14 (McCune & Mefford 1999) and SAS for Windows (Anon. 1999).

More detailed information with focus on the different research topics will be found in the material and methods sections of the chapters 4, 5, 6 and 7.

4 Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes

Stephanie Bissels, Norbert Hölzel, Tobias W. Donath & Annette Otte

Biological Conservation 118: 641-650

4.1 Abstract

Along the northern Upper Rhine, Germany, large-scaled restoration attempts aiming at the recovery of species-rich alluvial meadows from ex-arable fields were evaluated. We analysed floristic composition, soil nutrient status and biomass production of old and newly established meadows with respect to their position in both, the recent functional flood-plain and the fossil flood-plain compartment which is protected from flooding by a dyke. It is hypothesised that restoration in terms of species-enrichment will be more successful in the functional flood-plain due to the input of propagules in the course of flooding events.

Generally, we found great floristic differences between old and new meadows, independent of their position in the flood-plain. After 15-20 years of restoration management, the floristic structure of new meadows was still dominated by sown grasses and a high proportion of ruderal and arable species, whereas target species of flood-meadows largely failed to establish in both compartments. Old and new meadows differed only slightly in the environmental variables, while measured significant differences in plant available phosphorus and biomass yield were revealed between flood-plain compartments.

The results indicated a minor effect of edaphic site conditions on the low restoration success and limited dispersal and recruitment were revealed to be the main constraints for restoration. We found no evidence that species enrichment is enhanced in the functional flood-plain via the input of diaspores by flooding. Our results strongly suggest that dispersal limitation of target species is unlikely to be overcome merely by the restoration of more natural flooding conditions.

Keywords: Flood-plain; Dispersal; Hydrochory; Ordination.

4.2 Introduction

The reduction of soil fertility toward levels characteristic of existing species-rich target communities is often regarded as an essential precondition for the restoration of semi-natural grasslands of high nature conservation value (Kapfer 1988; Oomes 1990). However, in many recent grassland restoration projects, target species and communities did not re-establish at all, even after decades and successful lowering of the soil nutrient status and the biomass production at the restoration sites (Bakker 1989; Berendse et al. 1992; Bischoff 2002; Graham & Hutchings 1988). In such cases, the lack of propagules in the soil seedbank and limited dispersal of target species were identified as the main obstacles in the restoration of species-rich grasslands. Many target species are either not capable of forming a persistent soil seedbank or their seedbanks had been depleted by years of arable cultivation (Bakker 1989; Pfadenhauer & Maas 1987; Thompson et al. 1997). Thus, target species mostly have to immigrate from the surrounding area, a process which is often hampered by the absence of nearby viable source populations, a low seed rain and a lack of effective dispersal vectors in modern agricultural landscapes (Bakker & Berendse 1999; Bakker et al. 1996; Stampfli & Zeiter 1999; Verhagen et al. 2001).

Along the northern Upper Rhine large-scaled restoration measures aiming at the re-establishment of species-rich alluvial grasslands (alliance *Cnidion*) on former arable fields have been pursued for some 20 years. The reconnection of dyked areas to the natural flooding regime was thought to be an essential prerequisite for the fast restoration of former species richness, partly because diaspores are expected to be transported and deposited in the course of flooding events.

Flooding is widely regarded as a significant vector of dispersal in flood-plain ecosystems (Bakker et al. 1996; Bonn & Poschlod 1998; Johansson et al. 1996). In several studies large quantities of plant propagules were recorded in plant litter material of drift lines and sediment deposits created by flooding (Skoglund 1990). However, detailed information on the effectiveness of dispersal by flooding and its significance in restoration is still scarce.

We have been investigating this issue in a previous study along the northern Upper Rhine, concentrating on soil seedbanks (Hölzel & Otte 2001). Here, we extend this work by analysing the above-ground vegetation and several environmental variables to assess the significance of fluvial diaspore dispersal for species-enrichment at the restoration sites. Another impact of inundation by river water to be considered, is the input of nutrients via

sedimentation in the course of floods (Leyer 2002; Wassen et al. 2003), which could negatively affect the goal of lowering the soil nutrient status.

Due to the position of dykes, the study area is separated in two flood-plain compartments with different flooding regimes.

1. The **functional flood-plain,** comprising the land between the river and high winter dykes, is directly flooded up to a height of 3 m by water loaded with fine sediment during high water levels of the Rhine. As a consequence of this relatively natural flooding regime diaspores as well as nutrient containing sediments are expected to be transported and deposited during floods.

2. The **fossil flood-plain,** located on the landward site of the winter dykes is only submerged in low depressions (< 1 m) by ascending, clear and sediment-free groundwater during high water levels of the Rhine. Thus, the input of diaspores and nutrients by river water is precluded.

In this study, we compared restoration grassland in the functional and fossil flood-plain to see whether the goal of restoring former species-richness is enhanced or hampered by direct flooding. To get a reference for the restoration success, we also analysed existing species-rich old meadows in both flood-plain compartments. Floristic composition, soil nutrient status and biomass production were chosen as parameters to assess whether the restoration expectations have been fulfilled.

The following questions are addressed in this article: 1) To what extent did target species and -communities re-establish? 2) Which are the constraints that hamper restoration success? 3) Is the goal of restoration enhanced or hampered by direct flooding with river water?

4.3 Material and methods

Study area

The study area is situated in the Holocene flood-plain of the northern Upper Rhine about 30 km southwest of Frankfurt, Germany (N 49° 40'; E 8° 25'). The study sites are located in two adjacent nature reserves that contain approximately 450 ha of old species-rich flood-meadows and 300 ha of restoration grassland on ex-arable land.

The meadows of the studied type occupy fine-grained, calcareous alluvial soils and are irregularly flooded during high water levels of the Rhine. In conjunction with the warm and dry climate in the region, with mean annual precipitation 580 mm and mean annual temperature 10.3°C (Müller-Westermeier 1990), this leads to a high variability in soil water potential. While winter, spring and early summer may bring floods, summers are remarkably dry. Species composition of the old meadows that reflect the target community, is commonly referred to as *Allium angulosum* - *Alopecurus pratensis* - flood meadows (alliance *Cnidion*) with an average duration of flooding between 8 and 25 days per year, while higher elevations with short-term flooding are occupied by mesic alluvial *Arrhenatherion*-meadows (Hölzel 1999).

Until the 1950s (Knapp 1954) and even 1960s, species-rich alluvial grasslands that were managed extensively as hay-meadows dominated the whole area. Intensified drainage (since the 1920s) over the whole area, structural changes in agriculture and a series of dry years during the 1970s and 1980s accelerated the conversion into arable fields (Böger 1991). Starting in 1983 (functional flood-plain) and 1988 (fossil flood-plain), about 300 ha of arable land were converted into grassland. This was done mostly by natural regeneration but partly also by sowing with species-poor mixtures of common grasses or with freshly threshed material from species-poor, grass-dominated meadows. After the creation of a closed sward the meadows were managed extensively, i.e. mown from June onwards and no application of fertilizer. Sometimes the meadows are additionally grazed by sheep or mown for a second time in September or October.

Sampling of vegetation

On the basis of previous field work, all meadow allotments in the study area were stratified by flood-plain compartment (fossil/functional) and age (old/new). In 2001 we sampled 44 allotments in the functional flood-plain (22 old meadows, 22 new meadows) and 46 allotments in the fossil flood-plain (25 old meadows, 21 new meadows), which were well

scattered over the entire area. Since higher and therefore drier meadows were in both compartments preferentially converted into arable fields there might be a slight bias between old and new meadows with respect to flooding duration. Composition of vascular plant species was recorded on 100 m² plots usually situated in the centre of the meadows. Species abundance was estimated on a modified Braun-Blanquet-scale (van der Maarel 1979).
In June 2001 in each 100 m² plot, the standing crop of 10 randomly distributed quadrats (0.1 m²) was cut near the soil surface. The plant material was dried at 60 °C for 48 h and weighed to determine dry matter yield.

Soil nutrient analysis

Soil samples were collected by randomly taking 5 cores of 10 cm depth and 3 cm diameter within each plot. Plant available P and K were determined using the Calcium-Acetate-Lactate extraction method (CAL) according to Hoffmann (1991); total nitrogen and total carbon using a CN-analyser (FlashEA 1112, Thermoquest). The $CaCO_3$ content of the soil was measured using the method of Scheibler (Hoffmann 1991) and was used to calculate the organic matter content, and the C/N-ratio was estimated as a measure of nitrogen availability (Kuntze et al. 1994).

Data Analysis

To assess gradients in the vegetation data we used DCA-ordination. The first axis had a gradient length of 3.15 and thus showed a modest amount of unimodality (Legendre & Legendre 1998; Ter Braak & Smilauer 1998). Abundance data were square root transformed prior to analysis and species with less than three occurrences were excluded to reduce their unduly influence on the ordination result. The vegetation data were also used to calculate cover weighted means of the Ellenberg indicator values for moisture and nitrogen (Ellenberg et al. 1992). Correlations between axes scores and environmental variables were analysed using Spearman rank correlation.
Individual species that respond differently in new or old meadows, in either the functional or the fossil flood-plain, were identified by Indicator Species Analysis (Dufrêne & Legendre 1997). The values obtained were tested for significance by Monte-Carlo-Permutation tests with 5000 runs. We chose a threshold level of 25% for the index (Dufrêne & Legendre 1997) and only species with significant indicator values of at least 25 were listed. DCA-ordination, Indicator Species Analysis and associated calculations were performed using the software package PC-ORD 4.14 (McCune & Mefford 1999).

In order to adjust the Indicator Species Analysis and to exclude the potential bias towards higher moisture in old meadows, we performed a decomposition of variance by partial redundancy analysis (RDA). In the analysis, the Ellenberg indicator value for moisture was used as covariable with age (old/new) and flood-plain compartment membership of the meadows as explanatory variables. RDA was calculated with the program CANOCO (Ter Braak & Smilauer 1998).

Significant differences in site parameters between groups of samples were assessed using one-way ANOVA, with age (old/new) and compartment membership (functional/fossil) of the meadows as fixed effect. Proportions were angular transformed, ratios log-transformed and the remaining variables square-root transformed prior to analysis (Zar 1999). In case of significant differences the Tukey-Test for unequal sample sizes was employed. ANOVA and associated tests were carried out with STATISTICA 6.0 (Anon. 1998).

4.4 Results

Comparison of species composition

DCA-ordination (Fig. 1a) revealed a clear separation of old and new meadows irrespective of compartment affiliation along the first two axes. The samples from old meadows showed a much wider scatter, while new meadows were clumped in the lower left quadrant. There was also a separation between samples from the fossil and the functional flood-plain with the latter being generally placed closer to the upper right corner. The floristic structure of new meadows (Fig. 1b) was dominated by a limited number of species while old meadows were characterised by numerous species with a high range of variation.

Indicator Species Analysis resulted in many floristic indicators for old as well as for new meadows (Table 1).

Variance partitioning in RDA revealed that 11.8 % of the total variance was explained solely by the effect of moisture. The first two axes accounted for only 15.9 % of the variance in species data and showed that age of meadows and flood-plain compartment per se slightly affected species distribution. Although the effect of moisture was excluded, species that were highly correlated with old or new meadows (Fig. 2) corresponded largely with species found by Indicator Species Analysis (Table 1). Only a few species (e.g. *Carex acutiformis, Dactylis glomerata*) were revealed to be rather associated with the flood-plain compartment than with the age of the meadows.

Comparison of site parameters

Fig. 1 illustrates the correlations between the axes found by DCA and environmental variables. The first axis had a highly positive correlation with the Ellenberg moisture value and was negatively correlated with the percentage of therophytes (Fig. 1a, Table 2). The second axis displayed differences in soil nutrient richness, indicated by a negative correlation with the content of soil extractable P and K and the Ellenberg nitrogen value.

With respect to a large number of environmental variables ANOVA revealed highly significant differences between the four groups of samples (Table 3). Multiple comparisons showed that environmental variables differed only slightly between old and new meadows. Only potassium showed significantly higher values in the new meadows of the functional flood-plain.

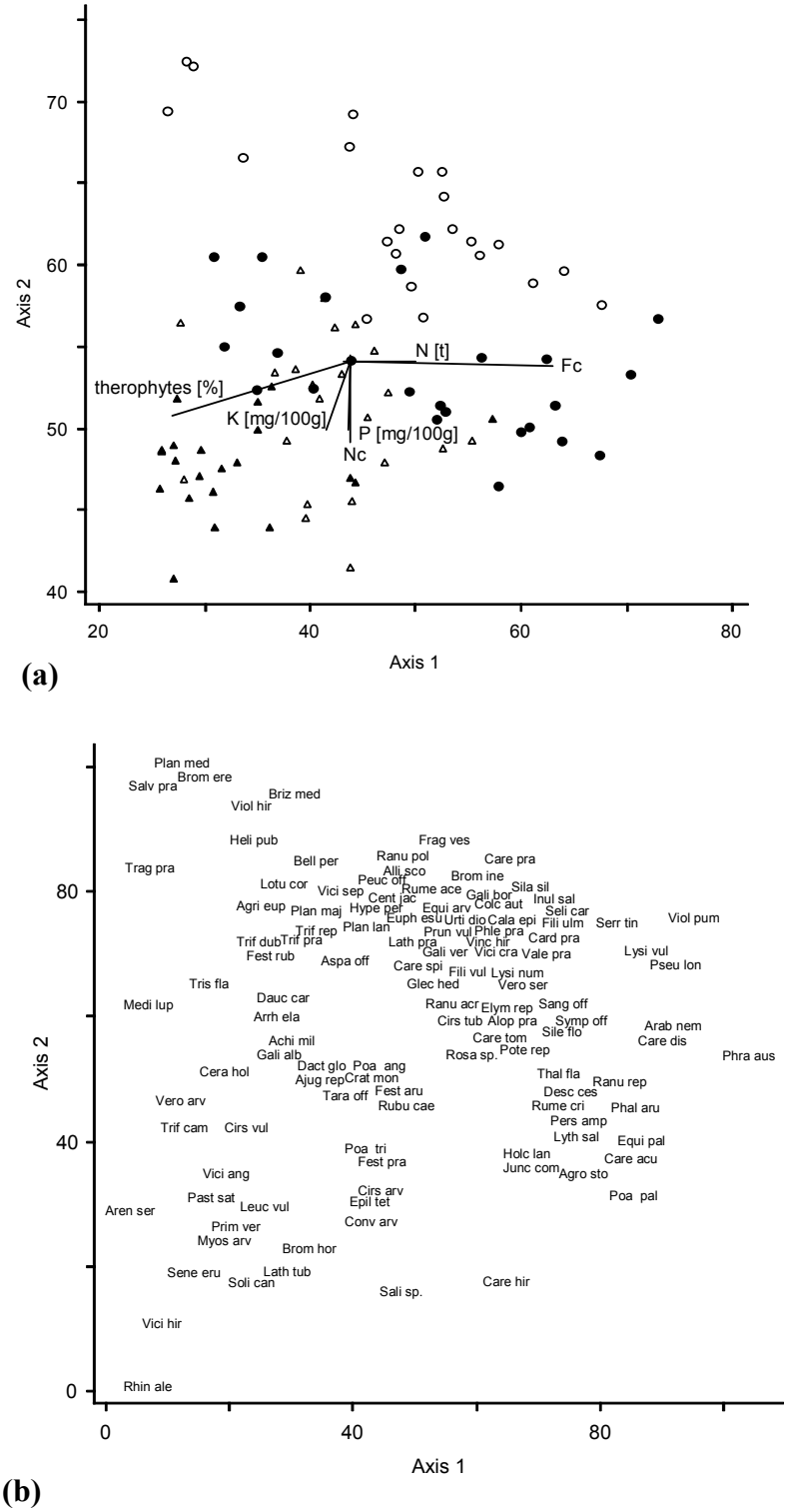

Fig. 1. DCA-ordination diagrams. **a)** Jointplot of vegetation relevés of old and newly created meadows in the fossil and the functional flood-plain. Correlations between DCA-axes scores and environmental variables are given as vectors. Circles = old meadows, triangles = new meadows, filled symbols = fossil flood-plain, open symbols = functional flood-plain; F_c = Ellenberg indicator value for moisture, N_c = Ellenberg indicator value for nitrogen, N_t = total nitrogen, K = content of available Potassium, P = content of available Phosphorus, therophytes = percentage of therophytes per plot. **b)** DCA-scores of all species with more than two occurrences. Full species names are given in the appendix.

Table 1. Indicator species (after Dufrêne & Legendre 1997) of old and new meadows.

Old meadows (*n* = 43)					**New meadows (*n* = 47)**				
	IV	SBT	LF	AW		IV	SBT	LF	AW
Alopecurus pratensis	66.6***	1	H		*Taraxacum officinale*	68.3***	3	H	X
Lathyrus pratensis	63.5***	2	H		*Poa angustifolia*	59.8***	3	H	
Sanguisorba officinalis	59.6***	1	H		*Cirsium arvense*	55.1**	3	G	X
Vicia cracca	59.4***	1	H		*Poa trivialis*	53.3***	3	H/Ch	X
Symphytum officinale	46.8***	1	H		*Vicia angustifolia*	50.9***	3	Th	X
Rumex acetosa	42.3***	2	H		*Dactylis glomerata*	50.6*	2	H	
Ranunculus acris	37.2***	3	H		*Leucanthemum vulgare*	47.3***	3	H	
Potentilla reptans	36.4*	3	H		*Achillea millefolium*	44.5**	2	Ch	X
Carex disticha	31.9**	2	H		*Festuca pratensis*	43.6*	1	H/Ch	
Centaurea jacea	31.8***	2	H		*Trifolium campestris*	30.8**	1	Th	X
Carex acutiformis	31.2**	2	H		*Vicia hirsuta*	30.2***	3	Th	X
Peucedanum officinale	30.9***	1	H		*Senecio erucifolius*	29***	n.d.	H	
Lysimachia nummularia	30.9**	2	Ch		*Pastinaca sativa*	28.6**	n.d.	H	
Valeriana pratensis	30.6**	1	H		*Crataegus monogyna*	28.5**	1	Ph	
Silaum silaus	27.7***	1	H		*Bromus hordeaceus*	28***	1	Th	X
Ranunculus polyanthemos agg.	27.2***	3	H		*Cerastium holosteoides*	27.5*	3	Ch/Th	X
Phalaris arundinacea	26.6**	3	H		*Solidago canadensis*	25.6***	1	H	X
Allium scorodoprasum	26.6**	1	G						

Significance obtained by Monte-Carlo-Permutation Test is given at three levels: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. IV = Indicator Value; SBT = Seedbanktype (Thompson et al. 1997) [1 = transient, 2 = short-term persistent, 3 = long-term persistent, n.d. = no data]; LF = Lifeform (Grime et al. 1988) [Ch = chamaephyte, G = geophyte, H = hemicryptophyte, Ph = phanaerophyte, Th = therophyte]; AW = arable weeds.

In contrast, we found significant differences between the fossil and the functional flood-plain compartment. Plant available P and biomass yield were significantly higher in the fossil flood-plain, while there was no difference in the C/N-ratio. In each flood-plain compartment soil organic matter and total N tended to have lower values in the new meadows than in old meadows. In the fossil flood-plain, the Ellenberg moisture value was significantly greater in old meadows than in the new ones.

4.5 Discussion

Species composition in old and new meadows

The analysis of floristic composition revealed strong differences between old and new meadows. The DCA-plot indicated that generally new meadows were more uniform, while old meadows showed a much higher floristic variation along environmental gradients. The floristic structure of old meadows was well characterised along a moisture gradient, ranging from species of drier (e.g. *Bromus erectus, Briza media*) to those of wetter sites (e.g. *Pseudolysimachion longifolium, Carex disticha*). In contrast, within the new meadows a comparable differentiation was lacking. Their floristic composition was rather characterised by a high proportion of ruderal species, whereas target species of flood-meadows largely failed to establish. We interpret this situation as a clear indication that new meadows were not floristically saturated, probably because of dispersal limitation.

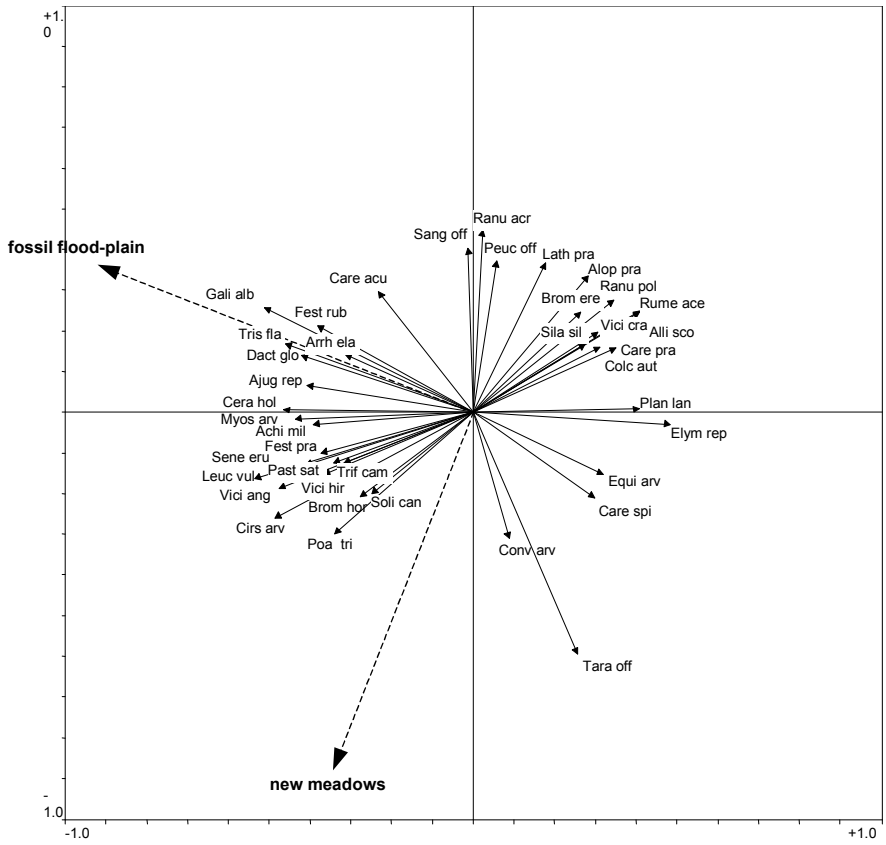

Fig. 2. Biplot based on Redundancy analysis (RDA) of the investigated meadows with respect to two environmental variables (age of the meadows, flood-plain compartment) and the effect of moisture (Ellenberg indicator value for moisture) as partialled out. The arrows for plant species (solid lines) and environmental variables (dashed lines) display the linear correlation coefficients between species abundance and the environmental variables. Full species names are given in the appendix.

Abiotic constraints

In contrast to other studies that stressed the importance of high nutrient levels for retarding species-enrichment we found only slight differences between old and new meadows in terms of soil nutrient properties and biomass yield. Various studies on the influence of nutrient availability on species richness in different grassland types indicate a dependency of species richness mainly on low P availability (Gough & Marrs 1990; Tallowin & Smith 2001; Venterink et al. 2001) or low P availability in combination with low K availability (Critchley et al. 2002; Oomes et al. 1996). Comparing the higher contents of plant-available K in new meadows with nutrient classes used in agricultural grassland management (Anon. 1993) the observed differences can be regarded as ecologically insignificant. The organic matter content and the content of total nitrogen within each flood-plain compartment was even lower in the new meadows than in the species-rich old meadows. This was probably due to former arable cultivation of the meadows that has reduced the organic matter pool (Gough & Marrs 1990). Generally, soil nutrient properties between old and new meadows are not sufficiently variable to explain the strong floristic differences we observed.

Table 2. Spearman correlation coefficients between environmental and biotic parameters and DCA-axes scores for samples (n = 90), *** $p \leq 0.001$.

	Axis 1	**Axis 2**
Moisture value (F_c)	0.59***	-0.13
Nitrogen value (N_c)	0.07	-0.49***
Biomass [g/m²]	0.03	-0.36***
Phosphorus [mg/100g]	-0.12	-0.55***
Potassium [mg/100g]	-0.36***	-0.44***
Organic C [%]	0.38***	-0.05
Total nitrogen [%]	0.36***	-0.04
C/N	0.15	0.19
Organic matter [%]	0.42***	0.03
Therophytes [%]	-0.7***	-0.37***

In contrast, we found great differences between the functional and the fossil flood-plain in terms of plant available P content and biomass yield with higher values in the fossil flood-plain. This was also reflected in a clear floristic separation between the meadows of both compartments. Since the depletion of fertilizer residues may require more than ten years (Gough & Marrs 1990; Tallowin et al. 1998), the considerable differences may result from the later cessation of fertilization in the fossil flood-plain (1988 compared to 1983 in the functional flood plain). In addition to a still raised nutrient availability, a better moisture supply due to more constant and higher groundwater tables in the fossil flood-plain may also contribute to an increase in biomass production.

Relatively low levels of soil nutrients and productivity do not support the idea that significant inputs of nutrients in the course of flooding may act as a constraint in restoration at our study plots. In contrast to our findings, Leyer (2002) observed strongly increased P levels in soils

Table 3. Mean values and standard error of site and vegetation parameters in old and new meadows of the functional and the fossil flood-plain. Different letters indicate significant differences, according to a Tukey-test (for unequal *n*) after one-way ANOVA. Asterisks display the significance levels revealed by ANOVA: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

	Functional flood-plain				Fossil flood-plain			
	Old (*n* = 22)		**New (*n* = 22)**		**Old (*n* = 21)**		**New (*n* = 25)**	
Number of species **	26.9 ± 1.9	a	20.4 ± 1.1	b	26.7 ± 1.8	a	27.4 ± 1.2	a
Moisture value (F_c) ***	5.5 ± 0.2	a	5.3 ± 0.1	a	6.2 ± 0.2	b	5.3 ± 0.1	a
Nitrogen value (N_c) ***	5.5 ± 0.1	a	5.7 ± 0.1	b	5.6 ± 0.1	b	5.6 ± 0.1	b
Biomass [g/m²] ***	455.9 ± 20.5	a	477.3 ± 16.7	a	682.0 ± 35.5	b	588.7 ± 23.7	b
Phosphorus [mg/100g] ***	4.8 ± 0.7	a	5.9 ± 0.4	a	12.8 ± 1.0	b	11.1 ± 0.5	b
Potassium [mg/100g] ***	7.6 ± 0.5	a	12.2 ± 0.9	b	8.7 ± 0.3	ac	10.3 ± 0.3	bc
Total nitrogen [%] ***	0.5 ± 0.1	b	0.2 ± 0.1	a	0.7 ± 0.1	c	0.4 ± 0.1	b
C/N *	10.4 ± 0.3	a	11.1 ± 0.2	a	10.7 ± 0.2	a	10.3 ± 0.1	a
Organic matter [%] ***	7.9 ± 0.3	b	4.3 ± 0.3	a	12.0 ± 0.6	c	7.9 ± 0.3	b
Therophytes [%] ***	2.7 ± 0.8	b	10.1 ± 1.7	a	2.7 ± 0.8	b	15.7 ± 1.5	a

of the functional flood-plain of the River Elbe, which she interprets as an effect of fluvial input due to the close proximity of the main river channel. The divergent results we obtained may be caused by the greater distance of our plots which were situated 500m to 4000m from the main water channel or from a large oxbow of the Rhine. According to Dister (1980) in the study area sedimentation rates during floods rapidly decline beyond the direct proximity of water courses, which suggests that our study sites are probably not affected by substantial nutrient loads. Furthermore alluvial forest that surround many of the studied meadows may act as a shelter against sedimentation.

Biotic constraints

The floristic differences between old and new meadows show up clearly in the Indicator Species Analysis and RDA. Old meadow sites were characterised by species adapted to relatively stable conditions, most of them hemicryptophytes, in particular grasses and sedges with predominantly vegetative means of dispersal. The results of Indicator Species Analysis (Table1) were verified by partial RDA, which confirmed that most of the indicator species are unaffected by moisture. Only *Carex acutiformis* lost its indicator function for old meadows after adjustment for moisture. The confinement of this species to the fossil flood-plain is mostly due to the more constant and higher ground water levels in this compartment (Leyer 2002).

Moreover, most of the indicator species of the old meadows are known to have a transient and short-term persistent seedbank (Bekker et al. 2000; Grime et al. 1988; McDonald et al.

1996; Thompson et al. 1997). In contrast, indicator species of new meadows were mostly ruderals typical of early successional stages (e.g. *Cirsium arvense, Bromus hordeaceus, Taraxacum officinale)*. A high proportion of these ruderal species can be seen as a heritage of former arable use. Most are either capable of forming large and long-lived seedbanks or they are adapted to wind dispersal, which are favourable traits for rapid colonisation in early stages of succession. Characteristic indicator species of new meadows also include some grasses (e.g. *Dactylis glomerata, Festuca pratensis*) that were introduced by sowing.

In accordance with other studies (Pywell et al. 2002; Smith et al. 2002) our results confirm that the creation of species-rich grassland on ex-arable land is highly seed limited and that there is little potential for the colonization by grassland species of later successional stages. However, even if target species occur in close proximity and have seeds adapted to wind dispersal (e.g. *Cirsium tuberosum, Peucedanum officinale, Serratula tinctoria*) diffusion to restoration sites is usually a relatively uncertain and time-consuming process (Bischoff 2002; Donath et al. 2003; Jensen 1998).

The impact of flooding on species establishment

We found no indication of a significant remote input of seeds by flooding events into the functional flood-plain. In contrast, the number of established species was even significantly lower than in the fossil compartment (Table 3). These results concur with a seedbank study in the same region by Hölzel and Otte (2001) who found only rare evidence for the input of diaspores in the seedbank during flooding events. Comparable conclusions were drawn by Bischoff (2002), who found that even in the proximity of remnant populations flooding does not significantly raise the dispersal distances.

In contrast, other studies showed that dispersal of seeds by water plays an important role to explain distribution patterns of riparian vegetation (Andersson et al. 2000; Goodson et al. 2002; Johansson et al. 1996; Skoglund 1990). However, such studies were usually conducted in close proximity to river channels and under much more natural hydrological and morphological conditions. Such flood-plains can be expected to have substantially more and spatially less isolated seed sources, than it is the case along the largely confined Upper Rhine (Thomas 1990). The strongly reduced number of potential source populations implies that dispersal in the course of flooding becomes a rare and highly stochastic event.

Conclusion for restoration management

As in many other grassland restoration projects we identified the lack of substantial seed sources as the main constraint in re-establishing former species-richness. Even in riparian ecosystems such as flood-meadows, dispersal limitation is unlikely to be overcome by the restoration of more natural flooding regimes under the present-day conditions prevailing along most Central European rivers.

Thus, the successful restoration of species-rich alluvial grasslands crucially depends on supplementary measures such as the sowing of seeds (Bosshard 2000; Pywell et al. 2002) or the transfer of propagules with plant material or transplants from species rich remnants (Šeffer & Stanová 1999; Hölzel & Otte 2003; Patzelt et al. 2001).

Acknowledgements

We are grateful to Josef Scholz-vom Hofe for his assistance in field work and in soil chemical analyses. We would also like to thank Lutz Eckstein for critical reading the manuscript and for helpful comments. This study was funded by the German Federal Agency for Nature Conservation.

Appendix:

Abbreviation	Species
Achi mil	*Achillea millefolium agg.*
Agri eup	*Agrimonia eupatoria*
Agro sto	*Agrostis stolonifera*
Ajug rep	*Ajuga reptans*
Alli sco	*Allium scorodoprasum*
Alop pra	*Alopecurus pratensis*
Arab nem	*Arabis nemorensis*
Aren ser	*Arenaria serpyllifolia agg.*
Arrh ela	*Arrhenatherum elatius*
Aspa off	*Asparagus officinale*
Bell per	*Bellis perennis*
Briz med	*Briza media*
Brom ere	*Bromus erectus*
Brom hor	*Bromus hordeaceus*
Brom ine	*Bromus inermis*
Cala epi	*Calamagrostis epigejos*
Card pra	*Cardamine pratensis*
Care acut	*Carex acutiformis*
Care dist	*Carex disticha*
Care hir	*Carex hirta*
Care pra	*Carex praecox*
Care spi	*Carex spicata*
Care tom	*Carex tomentosa*
Cent jac	*Centaurea jacea*
Cera hol	*Cerastium holosteoides*
Cirs arv	*Cirsium arvense*
Cirs tub	*Cirsium tuberosum*
Cirs vul	*Cirsium vulgare*
Colc aut	*Colchicum autumnale*
Conv arv	*Convolvulus arvensis*
Crat mon	*Crataegus monogyna s.l*
Dact glom	*Dactylis glomerata agg.*
Dauc car	*Daucus carota*
Desc ces	*Deschampsia cespitosa*
Elym rep	*Elymus repens*
Epil tet	*Epilobium tetragonum s.l.*
Equi arv	*Equisetum arvense*
Equi pal	*Equisetum palustre*
Euph esu	*Euphorbia esula*
Fest aru	*Festuca arundinacea*
Fest pra	*Festuca pratensis s.l.*
Fest rub	*Festuca rubra agg.*
Fili ulm	*Filipendula ulmaria*
Fili vul	*Filipendula vulgaris*
Frag ves	*Fragaria vesca*
Gali alb	*Galium album agg.*

Abbreviation	Species
Gali bor	*Galium boreale*
Gali ver	*Galium verum agg.*
Glec hed	*Glechoma hederacea*
Heli pub	*Helictotrichon pubescens*
Holc lan	*Holcus lanatus*
Hype per	*Hypericum perforatum*
Inul sal	*Inula salicina*
Junc com	*Juncus compressus*
Lath pra	*Lathyrus pratensis*
Lath tub	*Lathyrus tuberosus*
Leuc vul	*Leucanthemum vulgare agg.*
Lotu cor	*Lotus corniculatus*
Lysi num	*Lysimachia nummularia*
Lysi vul	*Lysimachia vulgaris*
Lyth sal	*Lythrum salicaria*
Medi lup	*Medicago lupulina*
Myos arv	*Myosotis arvensis*
Past sat	*Pastinaca sativa*
Pers amp	*Persicaria amphibia*
Peuc off	*Peucedanum officinale*
Phal aru	*Phalaris arundinacea*
Phle pra	*Phleum pratense*
Phra aus	*Phragmites australis*
Plan lan	*Plantago lanceolata*
Plan maj	*Plantago major*
Plan med	*Plantago media*
Poa ang	*Poa angustifolia*
Poa pal	*Poa palustris*
Poa tri	*Poa trivialis*
Pote rep	*Potentilla reptans*
Prim ver	*Primula veris*
Prun vulg	*Prunella vulgaris*
Pseu lon	*Pseudolysimachion longifolium*
Ranu acr	*Ranunculus acris*
Ranu pol	*Ranunculus plolyanthemos agg.*
Ranu rep	*Ranunculus repens*
Rhin ale	*Rhinanthus alectorolophus*
Rosa sp.	*Rosa spec.*
Rubu cae	*Rubus caesius agg.*
Rume ace	*Rumex acetosa*
Rume cri	*Rumex crispus*
Sali sp.	*Salix spec.*
Salv pra	*Salvia pratensis*
Sang off	*Sanguisorba officinalis*
Seli car	*Selinum carvifolia*
Sene eru	*Senecio erucifolius*

Abbreviation	Species
Serr tin	*Serratula tinctoria*
Sila sil	*Silaum silaus*
Sile flo	*Silene flos-cuculi*
Soli can	*Solidago canadensis*
Symp off	*Symphytum officinale s.l.*
Tara off	*Taraxacum officinale agg.*
Thal fla	*Thalictrum flavum*
Trag pra	*Tragopogon pratensis s.l.*
Trif cam	*Trifolium campestre*
Trif dub	*Trifolium dubium*
Trif pra	*Trifolium pratense*
Trif rep	*Trifolium repens*
Tris fla	*Trisetum flavescens*
Urti dio	*Urtica dioica*
Vale pra	*Valeriana pratensis*
Vero arv	*Veronica arvensis*
Vero ser	*Veronica serpyllifolia*
Vici ang	*Vicia angustifolia*
Vici cra	*Vicia cracca agg.*
Vici hir	*Vicia hirsuta*
Vici sep	*Vicia sepium*
Vinc hir	*Vincetoxicum hirundinaria*
Viol hir	*Viola hirta*
Viol pum	*Viola pumila*

5 Ephemeral wetland vegetation in irregularly flooded arable fields along the northern Upper Rhine: the importance of persistent seedbanks

Stephanie Bissels, Tobias W. Donath, Norbert Hölzel & Annette Otte

Phytocoenologia, in press

5.1 Abstract

Along the northern Upper Rhine ephemeral wetland vegetation is not confined to primary habitats such as the fringes of backwaters and river banks, but is also found in irregularly flooded arable fields. Within these highly variable environments, where disturbance is not only by flooding but also by agricultural management, we assessed the role of seedbanks for the persistence of ephemeral vegetation. In order to achieve this, we analysed the floristic composition of the above-ground vegetation and the corresponding soil seedbank of arable fields after a long-lasting spring and early summer flood in 2001. Moreover, we compared our vegetation data with other phytosociological studies from primary and secondary habitats along the northern Upper Rhine.

The comparison between primary and secondary habitats of mudflat species revealed differences in species composition. While primary habitats were characterized by the predominance of species of Isoëto-Nanojuncetea and Bidentetea, secondary habitats contained additionally species of the classes Agrostietea and Stellarietea.

The studied soil seedbanks were dominated by species typical of both, mudflat and agricultural habitats. Most species found in the seedbank were characterized by short life cycles and the ability to rapidly exploit periods of favourable conditions for germination and growth. The flooding treatments that were applied prior to the third season of seedbank analysis almost generally resulted in a high proportion of additional germination of mudflat species, even two years after the start of the analysis. The emergence of some mudflat species such as *Gnaphalium uliginosum*, *Veronica peregrina* and semi-aquatic helophytes such as *Alisma lanceolatum* and *A. plantago-aquatica* was actually confined to the flooding treatment.

Seed densities were exceptionally high and increased with the duration and frequency of inundation at the sampling sites. *Juncus bufonius*, *Ranunculus sceleratus* and *Veronica*

catenata were the most abundant species. For *Juncus bufonius* we found a maximum seed density of 707072 seeds/m², which is to our knowledge the highest seed concentration that was ever found in a higher plant. The large persistent soil seedbanks proved to be of outstanding importance for the emergence of ephemeral wetland vegetation after flood disturbances in arable fields. This was also reflected by the relatively high similarity between the seedbank and the established vegetation directly after flooding.

Our study highlights the importance of irregularly flooded arable fields as a secondary habitat for the conservation of ephemeral wetland species. At these sites, not only improved drainage and landfill threatens the occurrence of mudflat vegetation but also the replenishment of the seedbank is often prevented by early re-ploughing of the fields.

Keywords: Flood-plain; Germination; Inundation; Isoëto-Nanojuncetea; Mudflat vegetation.

5.2 Introduction

In riverine wetlands strong seasonal and interannual fluctuations of the water level may cause distinct vegetation dynamics along elevational gradients. Extended inundation at higher elevation that leads to a complete or partial dieback of the established canopy as well as periods of drought that create mudflats at the fringes of water bodies are typical situations that provide temporary suitable conditions for ephemeral wetland vegetation (Abernethy & Willby 1999). Due to the irregularity and unpredictability of such events persistent soil seedbanks play an important role along lowland rivers and largely determine the vegetation directly after drawdown. Thus, most ephemeral mudflat species are well known to build up large persistent soil seedbanks and are able to germinate directly after drawdown (van der Valk & Davis 1978; Casanova & Brock 2000; Jutila 2001). Beyond this, mudflat species have to rapidly complete their lifecycle and to refill the seedbank before the vegetation dies off when the soil dries out, succession proceeds or another disturbance occurs.

There are numerous studies on seedbanks of temporary marshes and tidal freshwater wetland (van der Valk & Davis 1978; Leck & Graveline 1979; Smith & Kadlec 1983; Ter Heerdt & Drost 1994; Leck & Simpson 1995). Contrary, relatively little information exists about the seedbanks of riverine wetlands (Schneider & Sharitz 1986; Abernethy & Willby 1999; Goodson et al. 2001, 2002), and about mudflat vegetation of secondary habitats in particular. While seedbank analysis of temporarily drained ponds were conducted by, e.g., Poschlod et al. (1996), seedbank studies of ephemeral wetland vegetation in secondary habitats along rivers are completely missing. Low-lying arable fields landwards the dykes constitute such secondary habitats along the northern Upper Rhine. An early description of the floristic composition of ephemeral plant communities in this particular situation was given by Oesau & Froebe (1972). This study revealed that irregularly flooded arable fields along riparian corridors comprise an important but so far neglected secondary habitat of ephemeral wetland vegetation. Presently, we have little knowledge whether agricultural intensification and changes in hydrology may adversely influence the persistence of these habitats. In this context long-term persistent soil seedbanks must be considered as a key factor to ensure the survival of mudflat species over periods of intense arable use.

In the present study we recorded the ephemeral mudflat vegetation in arable fields in the flood-plain of the northern Upper Rhine and analysed the role of the seedbanks in this habitat. All fields were situated on the landward site of high winter dykes (fossil flood-plain) and lower summer dykes (hybrid flood-plain), respectively. However, during high water levels of the Rhine shallow depressions in all fields under study are inundated by ascending, clear and

sediment-free groundwater and in the hybrid flood-plain also by high floods that spill over the low summer dykes. The subsequent drawdown leads to germination and establishment of mudflat species in open patches of the arable fields where a dieback of the crop has taken place during flooding.

The main objectives of this study were (i) to analyse the floristic composition of mudflat communities on arable fields and to compare them with similar phytosociological units from primary habitats, (ii) to assess species composition and size of the seedbank, and (iii) its relation to above-ground vegetation, water regime and management.

5.3 Study area

All arable fields under study were situated in the Hessian portion of the Holocene flood-plain of the River Rhine about 30 km south-west of Frankfurt, Germany (8°24'08'' E to 8°26'20''E and 49°50'20''N to 49°52'02''N; 83.9 m to 85.1 m a.s.l.) east of the main channel. Across the whole area, calcareous and extremely fine-grained alluvial soils topping sandy sediments of the Rhine, are predominant (Böger 1991). The climate of the region is relatively warm and dry, with a long growing season (> 250 days with mean temperature > 5°C), a high mean temperature of 10.3 °C and a low mean annual precipitation of 580 mm (Müller-Westermeier 1990). These climatic and hydrological conditions result in a highly variable soil water potential: while winter, spring and early summer may bring floods, the summer period is notably dry. Additionally, due to the high clay content (> 60%) plant-available water is rapidly declining shortly after the retreat of water.

Until the 1950s (Knapp 1954) and even 1960s this area was dominated by species-rich alluvial grasslands extensively managed as hay-meadows. With the start of intensified drainage in the 1920s, structural changes in agriculture and a series of dry years during the 1970s and early 1980s, the arable use was increasingly extended even to the lowest parts of the area (Böger 1991). Especially these depressions are prone to the effects of indirect flooding through a rising ground-water table in the hybrid and fossil flood-plain (up to 1 m). Along with the strong seasonal and inter-annual fluctuations of the water level of the River Rhine goes a maximum amplitude of the ground-water table of more than 6 m (Dister 1980; Böger 1991). The closer the sites are situated to the main channel the faster the ground water table rises or falls in accordance to the water regime of the Rhine, while distant sites are characterized by a more stable water regime (Fig.1). As a consequence, areas at the same elevation will be subject to longer periods of inundation close to the river channel than further

away (Table 1). High water levels from March until June are crucial for the successful reproduction of mudflat species, since flooding during winter and early spring with a drawdown before March will give farmers the option to re-plough and re-seed the mudflat habitats. In the period between 1980 and 2000 water regimes facilitating the development of ephemeral wetland vegetation occurred six times (on average every 3.5 years) with at most seven years in between. In 2001 the duration of inundation on sites close to the main channel of the river lasted at least two times as long and at distant sites up to five times as long compared to the period 1980 to 2000 (Table 1).

Table 1. Average time (weeks per year) in the period 1980 to 2000 and number of weeks in 2001 during which the ground water table was raised between March and June above different ground levels (m a.s.l.) at a sites close (C; 225 m) and distant (D; 1690 m) to the main channel of the river Rhine.

	1980 - 2000 yr.$^{-1}$		2001	
m a.s.l.	C	D	C	D
83.9	8.2	1.6	14	8
84.2	4.6	0.1	10	0
84.5	1.6	0	5	0
84.8	0.2	0	0	0
85.1	0.1	0	0	0

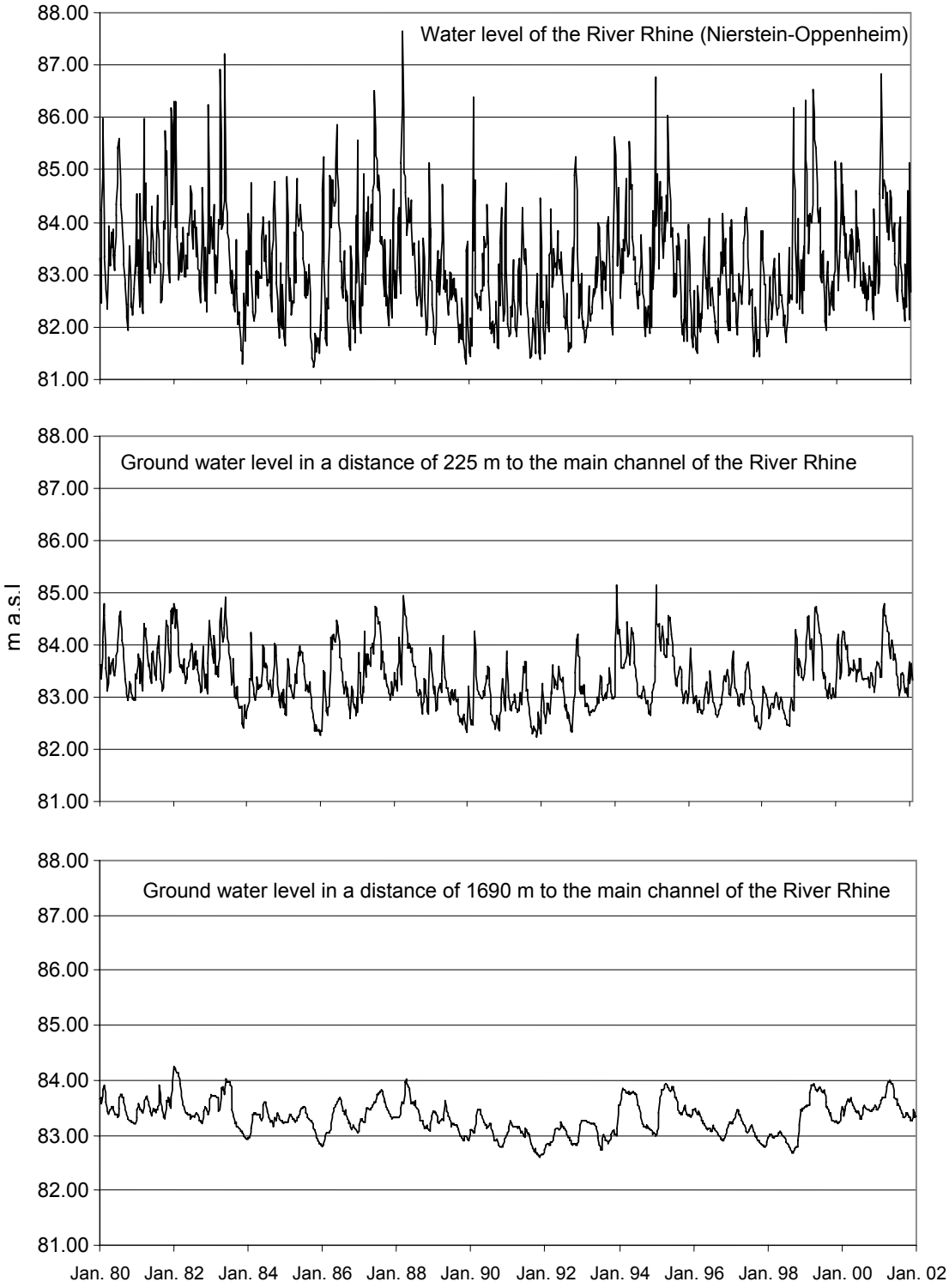

Fig. 1. Trend of the water level of the River Rhine and the groundwater level in two different distances to the main channel of the Rhine in the period 1980 to 2001.

5.4 Material and methods

Above-ground vegetation

We sampled the composition of vascular plant species in 32 plots of 25 m^2 (5 x 5 m) in June 2001. These relevés constituted an almost complete collection of ephemeral wetland vegetation of secondary habitats in the area, only some sites which were already re-ploughed by the time of the study could not be recorded. At all sites under study, the seeded crops had died back and were subsequently replaced by ephemeral wetland vegetation. Species abundance was estimated on a modified Braun-Blanquet-scale (van der Maarel 1979). Nomenclature of plant species follows Wisskirchen & Haeupler (1998).

Additionally, we compared the floristic composition of mudflat vegetation in arable fields of the present study, with phytosociological data from primary and secondary habitats along the northern Upper Rhine. We used vegetation relevés from temporary flooded arable fields by Oesau & Froebe (1972) and compared these with relevés of primary habitats (Oesau 1972; Dister 1980; Oberdorfer 1992). Phytosociological classification of the species follows Oberdorfer (1983, 1992).

Seedbank

At nine sites where above-ground vegetation was sampled, we also took samples of the soil seedbank. Using a soil corer of 3 cm diameter, at each site 20 cores of 10 cm depth were taken at random locations after removing all plant material from the soil surface. The soil samples represent 141 cm^2 of the soil surface and 1410 cm^3 of the soil volume in each allotment.

We analysed seedbanks with the seedling emergence method over 30 months (Roberts 1981). After removing vegetative plant material the soil samples were transferred to 18 cm x 28 cm Styrofoam trays as a 3 cm thick layer and exposed in free air conditions. The trays were protected against diaspore input and heating by covering them with flat, white gauze lids. Control basins filled with sterile soil were placed between the samples. Germinating seedlings were identified and removed once every week. Unidentifiable specimens were transferred to pots and grown until they could be named. When germination declined the samples were, after removal of emerging seedlings, regularly crumbled and mixed. To acquire both, the extent of the seedbank of common agrestal species, regularly occurring at terrestrial sites, and the seedbank of the typical ephemeral wetland vegetation, we exposed the samples to different water regimes. For the first 18 month the samples were exposed to terrestrial conditions with no flooding but regular watering to keep them moist. In accordance to findings by several authors (e.g., Ter Heerdt et al. 1999; Moravcova et al. 2001) who stress

the importance of stratification under amphibious conditions for the emergence of ephemeral wetland species, prior to the third season of the analysis the samples were first shallowly flooded for three months (January to March) and subsequently kept under waterlogged conditions.

Data analysis

From the vegetation relevés, we derived cover-weighted means of the Ellenberg values for moisture (Ellenberg et al. 1992). Topography of the respective sites and weekly data from the nearest ground water gauge were used to calculate flooding duration for the years between 1980 and 2000 and for 2001, the year of sampling.

Detrended Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples. To reduce their unduly influence on ordination results, rare species (i.e. occurrence in less than 20% of the samples) were down weighted (McCune & Mefford 1999). Prior to analysis the values of species abundance were transferred to a fully numerical 1-9 scale (van der Maarel 1979). Correlations between measures of water regime at the sample sites and the DCA sample scores were analysed with Pearson correlation as suggested by McCune & Mefford (1999).

The Mantel test (Legendre & Legendre 1998) was used to evaluate the similarity between the seedbank and the established vegetation as well as to test for spatial proximity in the vegetation and the seedbank. In the latter case we used analogous to the distance measure in space, the Euclidean distance measure to create the seedbank and vegetation matrices, but comparing seedbank and vegetation composition we used the Sørensen index. To test for the significance of the results we used the randomisation method (3000 runs; McCune & Grace 2002). Prior to the Mantel test the estimated species coverage was replaced by the percentage of the respective class of the Braun-Blanquet scale (van der Maarel 1979).

Effects of the flooding treatment on seedling emergence were tested with the non-parametric Mann-Whitney U-test. Correlations between seedbank density and elevation, as a measure of the overall prevailing water regime, were analysed using the Spearman rank correlation.

For correlations and other basic statistical analyses we used the software package STATISTICA 6.0 (Anon. 2002). DCA, Mantel test and the related statistical verifications were done with PC-Ord 4.14 (McCune & Mefford 1999).

5.5 Results

Above-ground vegetation

The DCA ordination had a total inertia of 1.95. The gradient length of axis 1 and 2 both exceeded two standard deviation units: 2.29 and 2.01, respectively. The first axis had the eigenvalue 0.25, while the eigenvalues of axis 2 and 3 were lower (0.16 and 0.12). The DCA ordination graph (Fig. 2) showed a separation of the plots according to the crops, which were originally cultivated at the respective sites. While sites with winter cereals are predominately positioned in the lower right corner, sites with rape, mustard and fallow land were situated in the upper left corner. The Pearson correlation coefficient between sample scores and direct as well as indirect parameters of the prevailing water regime showed clear trends along the axes 1 and 2 (Table 2). The Mantel test indicated a weak, albeit not significant, resemblance between the distance of the sites in space and the distance in vegetation composition of all samples ($r_{Mantel} = 0.14$, $P = 0.095$).

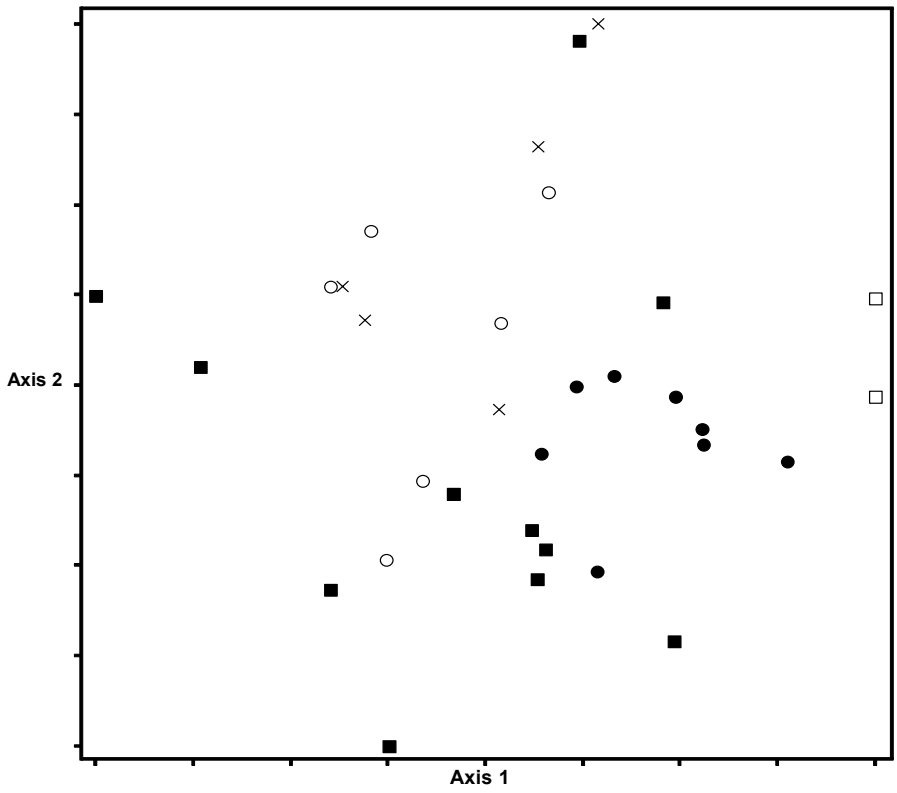

Fig. 2. DCA ordination diagram with scores of all relevés plotted along axes 1 and 2. Different symbols represent different crops cultivated on the arable fields under study: Winter crops are represented by filled symbols, i.e. circles in the case of winter barley and squares in the case of winter wheat. Rape and mustard are represented by empty circles and squares, respectively. Fallow land is represented by crosses.

Table 2. Pearson correlation between sample scores on the first two DCA axes and site parameters (N = 32).

	Axis 1	Axis 2
Moisture value	-0.32	-0.34
Elevation	0.45	-0.22
Weeks of inundation (1980-2001)	-0.47	-0.31

Comparison of floristic composition with similar vegetation studies

The comparison between vegetation relevés of ephemeral wetland vegetation in primary and secondary habitats on arable fields along the northern Upper Rhine indicated some differences in species composition (Table 3). While characteristic species of the class Isoëto-Nanojuncetea like *Limosella aquatica* or *Gnaphalium uliginosum* showed high plot frequencies in primary habitats, these species were much rarer or absent in secondary habitats. *Cyperus fuscus* was found in primary as well as in secondary habitats and showed the highest plot frequency in the community described by Oesau & Froebe (1972), which was located in arable fields on the opposite side of the River Rhine. Some species of the class Bidentetea such as *Ranunculus sceleratus* and *Rorippa palustris* occurred in both, primary habitats and in the arable fields under study. Additionally individual species of the class Phragmitetea were more often found in primary habitats (e.g., *Rorippa amphibia*) while others were clearly associated with secondary habitats (e.g., *Alisma lanceolatum*). Most characteristic to the arable field sites was the occurrence of species of the class Agrostietea (*Rorippa sylvestris*, *Agrostis stolonifera*) and a large number of arable weeds such as *Sonchus asper*, *Chenopodium polyspermum* or *Kickxia elatine*, which were completely absent in primary mudflat habitats. This also led to slightly higher species-richness per plot in the secondary habitats.

Table 3. Plot frequencies (%) of mudflat species in primary and secondary habitats in the northern Upper Rhine region based on four surveys: 1 = Oesau 1972 (in Oberdorfer 1992), 2 = Dister 1980, 3 = Oesau & Froebe 1972, 4 = present study; (M) = mosses; n.m. = not mentioned. Phytosociological classification follows Oberdorfer (1983, 1992).

	Primary habitats		Secondary habitats	
	1	**2**	**3**	**4**
Total number of relevés	214	9	17	32
Mean number of species	n.m.	11	13	14
Min number of species	n.m.	6	5	7
Max number of species	n.m.	20	19	26
Isoëto-Nanojuncetea				
Limosella aquatica	100	78	12	6
Cyperus fuscus	23	33	100	22
Gnaphalium uliginosum	64	78	.	3
Riccia cavernosa (M)	72	.	.	.
Physcomitrella patens (M)	59	.	.	.
Botrydium granulatum (M)	60	.	.	.
Centaurium pulchellum	.	.	24	6
Juncus bufonius	.	.	35	94
Lythrum hyssopifolia	.	.	24	.
Bidentetea				
Chenopodium rubrum	37	22	.	.
Ranunculus sceleratus	58	89	12	66
Persicaria lapathifolia	.	22	47	100
Rorippa palustris	.	56	18	22
Atriplex hastata	.	11	12	19
Rumex maritimus	.	22	.	3
Alopecurus aequalis	.	67	.	.
Rumex palustris	.	11	.	.
Persicaria minus	.	11	.	.
Potentilla supina	.	.	24	.
Bidens tripartita	.	.	12	.
Phragmitetea				
Rorippa amphibia	31	100	.	.
Oenanthe aquatica	1	44	.	3
Carex gracilis	.	44	.	.
Phalaris arundinacea	.	11	.	3
Schoenoplectus lacustris	.	11	.	.
Iris pseudacorus	.	11	.	.
Alisma plantago-aquatica	.	.	41	6
Alisma lanceolatum	.	.	24	19
Typha latifolia	.	.	35	3
Phragmites communis	.	.	18	.
Veronica anagallis-aquatica	.	.	12	.
Agrostietea				
Rorippa sylvestris	.	.	59	44
Rumex crispus	.	33	.	22
Agrostis stolonifera	.	.	18	13
Potentilla reptans	.	.	12	.

	Primary habitats		Secondary habitats	
	1	**2**	**3**	**4**
Stellarietea				
Euphorbia platyphyllos	.	.	35	.
Sonchus arvense	.	.	12	.
Persicaria aviculare	.	.	47	81
Sonchus asper	.	.	24	44
Persicaria maculosa	.	.	41	22
Chenopodium polyspermum	.	.	12	38
Kickxia elatine	.	.	29	6
Stellaria media	.	.	12	3
Chenopodium album agg.	.	.	12	3
Echinochloa crus-galli	.	.	.	34
Alopecurus myosuroides	.	.	.	25
Anagallis arvensis	.	.	.	22
Atriplex patula	.	.	.	19
Tripleurospermum perforatum	.	.	.	13
Additional taxa				
Veronica peregrina	80	78		
Nymphoides peltata	10	11		
Populus nigra	.	22		
Veronica catenata	53	100	71	94
Salix alba	7	22	24	9
Plantago major agg.	.	22*	41	84*
Juncus articulatus	.	11	76	72
Persicaria amphibia		22	12	16
Epilobium tetragonum	.	.	35	53
Cirsium arvense	.	.	29	28
Lythrum salicaria	.	.	35	3
Poa trivialis	.	.	41	.
Stachys palustris	.	.	35	.
Samolus valerandi	.	.	24	.
Triticum aestivum	.	.	.	38
Epilobium hirsutum	.	.	.	22
Equisetum palustre	.	.	.	16
Agropyron repens	.	.	6	13
Brassica napus	.	.	.	13
Coronopus squamatus	.	.	.	13
Taraxacum officinale agg.	.	.	.	13
Mentha arvensis	.	.	12	.
Myosoton aquaticum	.	.	12	.

* *Plantago major* ssp. *intermedia*

Additional taxa: *Chenopodium hybridum* (rel. 3:6, 4:6); *Poa annua* (3:6, 4:3); *Ranunculus repens* (3:6, 4;3); *Potentilla anserina* (3:6); *Phalaris canariensis* (3:6); P*ortulaca oleracea* (3:6); *Chaenorrhinum minus* (3:6); *Senecio vulgaris* (3:6); *Avena fatua* (3:6); *Valerianella carinata* (3:6); *Apium nodiflorum* (3: 6); *Chenopodium ficifolium* (3:6); *Matricaria inodora* (3:6); *Sparganium ramosum* (3:6); *Scirpus maritimus* (3:6); *Symphytum officinale* (3:6); *Amaranthus retroflexus* (4:9); *Tussilago farfara* (4:9); *Apera spica-venti* (4:6); *Juncus compressus* (4:6); *Bolboschoenus maritimus* (4:6); *Capsella bursa-pastoris* (4:6); *Fallopia convolvulus* (4:6); *Fumaria officinalis* (4:6); *Kickxia spuria* (4:6); *Schoenoplectus tabernaemontani* (4:6); *Solanum nigrum* (4:6); *Sonchus oleraceus* (4:6); *Trifolium repens* (4:6)*; Veronica arvensis* (4:6); etc.

Seedbank

Altogether 28,724 seedlings emerged from the nine samples. The lowest calculated number of seedlings per square meter was 5022, while the highest total seed density was 761,961 seeds/m². On average we found 225,756 seeds/m^2 in the upper 10 cm of the soil. In five samples we found more than 100,000 seeds/m^2 of which three contained even more than 300,000 seeds/m^2. A total of 47 different plant species could be identified in the seedbank samples, with an average of 15.7 (11-23) different species per sample. *Juncus bufonius* was by far the most prominent species with the highest maximum seed density (Table 4). While the soil seedbank was dominated by short-lived species typical of agricultural, ruderal or ephemeral wetland habitats, long-lived species typical of low-lying flood meadows (e.g., *Juncus inflexus*, *J. compressus*, *Pseudolysimachion longifolium*) made up only a small portion.

The total number of seedlings in all samples emerging before and after experimental flooding did not differ significantly. However, when the group of ephemeral wetland species (N = 12) and the group of typical agricultural species (N = 35) were tested separately, only in the former a significant increase in seedling emergence was revealed (Mann-Whitney U-test, $P < 0.001$). In most species flooding of the samples caused a high number of additionally emerging seedlings (Table 4). Of the total 47 species, 23 did only emerge before and 10 only after flooding whereas 14 species were found during both phases. The correlation between the elevation as a measure for the moisture regime prevailing at the sites and the densities in the seedbank was significant ($r = -0.72$, $P \leq 0.05$).

The Mantel test indicated a weak, albeit not significant, resemblance between the spatial proximity of the sites and the seedbank composition ($r_{Mantel} = 0.23$, $P = 0.07$), but revealed a significantly positive resemblance between the seedbank and the vegetation composition of all samples ($r_{Mantel} = 0.34$, $P = 0.03$).

5.6 Discussion

Above-ground vegetation

Although the gradients found in DCA are relatively short, the grouping of the relevés in ordination space seems to be influenced by the originally seeded crop (Fig. 2). Different crops are commonly associated with a characteristic weed flora, with differences most pronounced between winter and summer crops (Cavers & Benoit 1989; Otte 1992). Although flooding may equalise differences of the associated weed flora (Zahlheimer 1979), it seems not to completely blot out differences. Differentiating effects of management may be owing to preparation of the seed bed, time of seeding and differences in the reaction of the crops towards flooding. As in fallow land, on rape fields coverage of the soil in spring is higher than under cereals. The resulting differences in light penetration may be high enough to induce a differentiation in species composition between fields originally sown with rape and cereals.

Beside the effects of the management also the prevailing water regime seems to influence the resulting mudflat vegetation (Table 2). This is in accordance with findings in seedbanks of temporary wetlands in New South Wales, where differences in the time of occurrence, duration and depth of flooding had a high impact on species composition of the above-ground vegetation (Casanova & Brock 2000). Although these effects even can be strong enough to overrule differences in the initial seedbank composition (Seabloom et al. 1998; Nicol et al. 2003) this seems not to be the case in the mudflat vegetation of the present study since the Mantel test revealed a significantly positive correlation between above-ground vegetation and the seedbank composition.

The higher importance of these two factors for the emerging mudflat vegetation is also confirmed by the Mantel test of the individual distances between the sites and above-ground vegetation, which suggests a high spatial variability. This variability is most likely induced by differences in water regime and management, which overrule similar climatic and edaphic conditions in the study area. Our findings are in accordance with other studies that also showed a particularly high spatial and temporal variability of mudflat vegetation in secondary, man-made habitats, such as fishponds (Poschlod et al. 1996; Šumberová et al. 2004).

Table 4. Characteristic parameters of the 30 most abundant species in the seedbank of ephemeral wetland vegetation in arable fields (N = 9) and reaction of the species to flooding. Significant differences in seedling emergence before and after experimental flooding of the samples are indicated by an asterisk (Mann-Whitney-test; $\alpha \leq 0.05$). min = minimum; max = maximum.

		Percentage of the total seedbank	Seedling density (m^{-2})			Plot-frequency	Emerged seedlings		
			Min.	Mean	Max.		before Flooding	After	after (%)
Juncus bufonius		85.9	1061	193,910	707,072	100	10,008	14,664	59
Ranunculus sceleratus		4.14	71	9337	33,458	89	618	570	48
Veronica catenata	*	2.73	1627	6162	19,099	100	624	160	20
Plantago intermedia	*	1.65	212	3733	12,591	78	438	37	8
Juncus articulatus		1.44	71	3262	6649	100	182	233	56
Chenopodium polyspermum	*	1.01	71	2279	7569	89	284	6	2
Persicaria lapathifolium	*	0.94	141	2114	13,157	89	257	12	4
Rorripa sylvestris		0.77	283	1729	12,025	33	195	25	11
Rorripa palustris		0.35	71	794	3820	56	79	22	22
Persicaria maculosa	*	0.17	71	393	1203	89	48	2	4
Alopecurus myosuroides	*	0.13	141	299	1698	56	38	0	0
Cyperus fuscus		0.1	71	236	920	44	21	9	30
Juncus inflexus		0.1	71	228	1,981	22	28	1	3
Amaranthus retroflexus	*	0.09	71	204	1203	44	26	0	0
Sonchus asper	*	0.07	71	149	495	67	17	2	11
Echinochloa crus-galli		0.05	0	102	920	11	13	0	0
Agrostis stolonifera	*	0.03	71	79	424	56	10	0	0
Persicaria aviculare		0.03	71	79	354	44	9	1	10
Gnaphalium uligonosum		0.03	71	63	495	22	0	8	100
Alisma plantago-aquatica		0.02	0	55	495	11	0	7	100
Sonchus arvensis		0.02	0	55	495	11	7	0	0
Veronica peregrina		0.02	0	47	424	11	0	6	100
Alisma lanceolata		0.02	71	39	283	22	0	5	100
Juncus compressus		0.02	0	39	354	22	0	5	100
Phacelia tanacetifolia		0.02	0	39	354	11	5	0	0
Veronica arvensis		0.02	141	39	212	11	0	5	100
Anagallis arvensis		0.01	0	31	283	11	4	0	0
Mentha aquatica		0.01	0	31	283	11	4	0	0
Solanum nigrum		0.01	0	31	141	22	4	0	0
Veronica persica		0.01	0	31	283	11	4	0	0

Floristic composition of primary and secondary habitats

The characteristic species of primary habitats, *Limosella aquatica*, is able to germinate immediately after drawdown and is therefore one of the first plants that occur in mudflat communities. But since *L. aquatica* relies on moist soil conditions for germination and establishment (Oesau 1972), it rapidly completes its life cycle during prolonged drawdown and is subsequently replaced by more drought-tolerant species (e.g., *Cyperus fuscus* and *Veronica peregrina*). This suggests that not flooding itself but the period of successive drawdown has a major impact on germination and also on floristic composition of mudflat communities (Casanova & Brock 2000; Nicol et al. 2003; Hölzel & Otte 2004a). In accordance to that, primary and secondary habitats differed also in soil composition; especially the typically high clay content (> 60%) of secondary habitats slows down the descend of the water. This is even amplified through their positioning in isolated depressions without superficial drainage. As supposed by Zahlheimer (1979) some species (e.g., *Lythrum hyssopifolia*) may rely upon these longer time periods with favourable soil moisture conditions and are therefore restricted to secondary habitats. Along the northern Upper Rhine species such as *Juncus bufonius*, *Centaurium pulchellum* or *Samolus valerandi* predominantly occurred in arable fields, which is probably due to the slower retreat of the water at these sites that gives these species a wider time frame for germination, growth and reproduction. In contrast to primary habitats, mudflat communities of secondary habitats contain a higher number of species from related vegetation classes, such as Agrostietea, Phragmitetea or Stellarietea. Many of them (i.e. *Rumex crispus*, *Persicaria aviculare*, *Chenopodium polyspermum*) build up persistent seedbanks and are thus well adapted to the conditions prevailing at the temporary flooded arable fields. Perennials such as *Rorippa sylvestris*, *Ranunculus repens* and *Agrostis stolonifera*, which rely on an extensive root system to re-grow after disturbances are successful in arable land but are apparently not able to tolerate long-lasting submersion related to the regular water regime of primary habitats. Since favourable conditions for germination, growth and reproduction of arable weeds do only occur in secondary habitats these species are lacking in primary habitats of Isoëto-Nanojuncetea communities. The tendency of higher species numbers found in secondary habitats is mostly due to the addition of arable weeds to the usual species pool of mudflats (van der Valk & Davis 1978).

Seedbank composition

Average species numbers in our samples agree with results from other temporal wetland habitats (van der Valk & Davis 1978; Leck & Graveline 1979; Smith & Kadlec 1983). In these studies, seedbanks were also dominated by rather few species while the dominance by a single species like *Juncus bufonius* is quite unusual. However, relatively high densities of *Juncus bufonius* in secondary habitats were also found by Bernhardt (1993). In a review, Leck (1989) showed that the seedbanks of wetlands are most often dominated by monocots with high longevity.

In the present study most species found in the seedbank were agrestal and mudflat species with high light requirements for germination, strict confinement to open habitats (Baskin & Baskin 2001) and the ability to reproduce within a short period of time. While growth and reproduction of mudflat species in natural habitats is mainly limited by the availability of favourable moisture conditions alone, in secondary habitats agricultural management further limits the development of such species. Usually farmers re-plough the sections of the fields which harbour mudflat species as soon as possible after the descend of the water. Thus in these secondary habitats not only the occurrence of inundation is important but also its duration, which has to last long enough to avoid re-cultivation until the species successfully reproduced.

The main strategies of the mudflat species to cope with this highly variable environment are to build up a persistent seedbank to bridge periods of unfavourable site conditions and to exploit the short time with favourable conditions for growth and reproduction (Bonis et al. 1995). Except for *Alopecurus myosuroides*, all species found in the seedbank are known to build up a long-term persistent seedbank (Grime et al. 1988; Thompson et al. 1997; Hölzel & Otte 2004b). During the irregular and relatively short appearance of mudflat species small-sized seeds are produced and released in large quantities. In temporarily drained ponds, e.g., Poschlod et al. (1996) found that the seed rain of *Alopecurus aequalis* and *Juncus articulatus* may consist of more than 300,000 seeds m^{-2} and in *Ranunculus sceleratus* a single plant may release up to 56,000 seeds m^{-2} (van der Toorn 1980). Additionally, mudflat species have very short life cycles. *Ranunculus sceleratus* only needs two month after germination until seed set and *Juncus bufonius* flowers within four weeks (Grime et al. 1988). Beyond this, species may react flexible to sub-optimal growing conditions. For example, late emerged individuals of the mudflat species *Chenopodium rubrum* were found to start flowering after a shorter time and at an earlier developmental stages (van der Sman et al. 1993).

Seedbank density

Seed densities in this study are on average much higher than those regularly found in comparable temporary habitats such as glacial marshes (van der Valk & Davis 1978), river marshland (Leck & Graveline 1979), freshwater tidal marshes (Leck & Simpson 1987), wetlands in South Australia (Nicol et al. 2003) or secondary habitats such as regularly drained ponds (Poschlod et al. 1996). Only few maximum densities in wet grasslands in southern Sweden (Skoglund 1990) and in an Appalachian Sphagnum bog (McGraw 1987) reached values in range with average seed densities found in our study. However, in the latter two studies samples were taken to a soil depth of more than 10 cm. The only two studies we know, in which densities of the diaspore bank were even higher, were conducted in Mediterranean temporary marshes in southern France (Bonis et al. 1995) and along the Guadalquivir in southern Spain (Grillas et al. 1993). But in both cases *Characeae* alone accounted for up to 98% of the total diaspore density. Apart from these habitats with strong natural dynamics, high seed densities are also expected to occur under the conditions of arable management, where seed contents can also reach levels of the above mentioned habitats (Jensen 1969; Cavers & Benoit 1989). In our study seed densities found in agricultural mudflat habitats were much higher than those reported from seedbanks of flood meadows in the same area (Hölzel & Otte 2001). In accordance with this study we found an increase in seed densities in the soil with increasing flooding duration that was also reported by other authors (c.f. Chippendale & Milton 1934; Thompson & Grime 1979). This general increase of seed densities may be seen as an adaptation to irregular and unpredictable disturbances that favour species following a ruderal strategy (Grime 2002).

A comparison of the obtained seed densities of individual species with data from the database by Thompson et al. (1997) showed that most seed densities are in the range of previous analyses, but in case of the three most abundant species i.e. *Juncus bufonius*, *Ranunculus sceleratus* and *Veronica catenata* the values distinctly exceeded the highest mean and maximum numbers found so far. Especially, the maximum seed density of 707,072 seeds m^{-2} for *Juncus bufonius* not only marks a new record for this species, but to our knowledge is, up to date, the highest seed density found in any higher plant (c.f. Thompson et al. 1997).

Influence of flooding

Among species that showed lower or no additional emergence of seedlings after flooding all but one (i.e. *Veronica catenata*) belong to the group of typical agrestal species in the region. While this can in part be attributed to adverse conditions for germination (i.e. too wet, low

oxygen levels; Baskin & Baskin 2001) another reason may be that in seedbank analyses most seedlings regularly emerge within the first year (Ter Heerdt et al. 1996; Thompson et al. 1997). Although this phenomena may be responsible for the higher number of species occurring before flooding than afterwards (23 vs. 10), it is quite astonishing that about 55% of all seedlings emerged after the flooding treatment despite the shorter time period under waterlogged conditions. Most obvious is the positive effect of this treatment in the germination of typical mudflat species such as *Gnaphalium uliginosum* and *Veronica peregrina* as well as the helophytes *Alisma lanceolata* and *A. plantago-aquatica*, in which all individuals emerged after the application of the flooding treatment. Findings by Moravcová et al. (2001) also highlight the importance of cold stratification and flooding for the germination of *Alisma lanceolata*, *A. plantago-aquatica* and *A. gramineum*.

These findings are in accordance to authors who stress the importance of an adequate treatment when assessing the soil seedbank in habitats known to harbour species groups with divergent requirements for germination (van der Valk & Davis 1978; Leck & Graveline 1979; Smith & Kadlec 1983; Gerritsen & Greening 1989). In our study the sequential application of different moisture treatments was found to be particularly useful and led to an increase of detected seeds of typical mudflat species.

Conclusions

Our results highlight the importance of irregularly flooded arable fields as a habitat for ephemeral wetland plant species and communities, which are partly considered as endangered (e.g. *Samolus valerandi*, *Centaurium pulchellum*, *Coronopus squamatus*; Korneck et al. 1996). Since in these strongly disturbed dynamic habitats, seedbanks are of major importance for the long-term preservation of such plant communities, measurements for their preservation have to aim at the maintenance and renewal of the seedbank. In contrast to mudflat plants in primary habitats, which are able to grow and reproduce also in years with only slight drawdown at exposed edges of oxbows and river banks, in secondary habitats successful reproduction and thus replenishment of the soil seedbank is restricted to years with extremely long lasting floods of the Rhine. Thus, reproduction is not only a priori less frequent than in primary habitats, but additionally at risk by human activities. Although in arable weeds generally adverse effects of fertilization and herbicide application are known (Roberts & Neilson 1981; Cavers & Benoit 1989; Otte 1992), the high seed densities and species numbers we found, suggest that the maintenance of the seedbank is not negatively influenced by intensive arable use.

Since farmers want to reduce the losses in crops caused by inundation fields they try to lower flooding frequency and duration by improved drainage or by landfill depressions with soil, which means a complete destruction of the habitat for wetland ephemerals (Täuber & Petersen 2000). After flooding and subsequent emergence of mudflat species from the seedbank it is essential that plants can successfully reproduce. Therefore, it is important to extent the period until the field is re-ploughed after the retreat of flooding water. In fact, even from the farmers' point of view there is no need to re-plough as soon as possible with the aim to reduce seed input. Since the emergence of mudflat species is confined to a relatively short period directly after flooding they are not a real problem for arable crop production anyway. Actually, the described secondary mudflat communities strictly depend on arable use. Without regular disturbances by ploughing the flood-plain levels these communities occupy in arable fields would be rapidly colonised by competitive perennial species. Thus, the preservation of these secondary mudflat communities crucially depends on a continuation of arable use at relatively low elevations in flood-plains.

Acknowledgements

We would like to thank Christiane Lenz-Kuhl and Josef Scholz-vom Hofe for their help in collecting and analysing the soil seedbank samples. We gratefully acknowledge the funding of our work by the German Federal Agency for Nature Conservation (BfN).

6 Effects of different mowing regimes and environmental variation on seedling recruitment in alluvial grasslands

Stephanie Bissels, Tobias W. Donath, Norbert Hölzel & Annette Otte

submitted

6.1 Abstract

The availability of suitable microsites for seedling recruitment is of high importance for successful restoration of semi-natural grassland communities. There are many environmental factors which may affect microsite quality, e.g. management practices are known to have a strong impact on safe sites. We investigated the effects of different mowing regimes on seedling recruitment of six typical flood-meadow herbs in seed addition experiments in two alluvial grasslands with different flooding regimes. One species-poor meadow was situated in the functional flood-plain and the other one in the fossil flood-plain which is protected against direct flooding by a dyke and only submerged by ascending groundwater. Treatments included three different mowing regimes: (i) mowing in September, (ii) mowing in June, (iii) mowing in May and August. Seedling recruitment was monitored for two years.

The applied management measures had only minor effects on the germination and establishment of the flood-meadow species. In both studied meadows low germination rates occurred, particularly in the small-seeded *Inula salicina,* suggesting a lack of suitable microsites in the sward. Significant effects of the different mowing regimes were only revealed in the first study year, when biomass production of the meadows was much higher than in the second study year. During this period mowing twice (May and August) led to higher seedling densities, suggesting competitive release from mowing.

Beyond weak effects of the applied treatments, physical hazards such as flooding and drought seemed to control seedling germination and establishment to a large extent. Our findings suggest that the high spatio-temporal variability of site conditions in flood-plains underline the high significance of occasionally occurring events of successful recruitment for the persistence of flood-meadow species.

Keywords: Flood-plain; Seedling establishment; Drought; Microsite limitation.

6.2 Introduction

In permanent grassland generative reproduction of perennial plants is, in contrast to clonal propagation, often considered to be a highly stochastic event (Harper 1977; Grime 2002). Many field experiments revealed rather low seedling densities and high mortality rates in the closed canopy of semi-natural grasslands (Silvertown & Dickie 1981). However, recruitment by seeds still contributes significantly to the population structure of long-lived herbaceous species, is important for genetic variation or long-distance dispersal (Watkinson & Powell 1993; Eriksson 1997) and thus determines population persistence.

Many studies have shown that seedling recruitment may be limited by the availability of seeds (Eriksson & Ehrlén 1992; Tilman 1997; Pywell et al. 2002) as well as by the lack of suitable microsites (Kotorová & Lepš 1999; Stampfli & Zeiter 1999; Isselstein et al. 2002). If seed limitation is precluded, e.g. by sowing seeds into a species-poor sward, there is still a number of interacting factors that may affect micro-site quality and hence seed germination as well as establishment of plant populations.

Disturbance in semi-natural grassland ecosystems, e.g. by management is known to have strong impact on the number of microsites (Bullock et al. 1994). Mowing e.g. reduces inhibition by living and dead plants (Foster 1999) and provides gaps in the sward that may enhance seedling establishment (Bakker et al. 1980; Hutchings & Booth 1996; Kotorová & Lepš 1999). In wetlands, flooding can be seen as another important type of disturbance but it is, in contrast to management, usually an irregular and unpredictable event. Flooding also creates gaps in the vegetation and prevents competitive exclusion (Bornette & Amoros 1996). However, due to anaerobic stress, long lasting inundation periods may also negatively influence survival and growth of seedlings (van den Brink et al. 1995; Blom & Voesenek 1996).

Flood-plain ecosystems constitute a highly variable environment: irregular floods in winter and spring may alternate with extended periods of summer drought. Such harsh abiotic conditions suggest that the sensitive seedling stage is the major constraint for recruitment. Furthermore, abiotic and biotic environmental conditions may vary between sites and years (De Jong & Klinkhamer 1988; Fowler 1988; Ryser 1993) and individual species may differ in their specific requirements during the recruitment phase (Kotorová & Lepš 1999). For the preservation and restoration of endangered alluvial grasslands, it is therefore important to know which factors or interactions affect recruitment by seeds.

We investigated seedling recruitment of six typical flood-meadow herbs with respect to different management types and flooding regime in seed addition experiments. The study sites comprised species-poor grassland swards which were situated in the functional flood-plain and in the fossil flood-plain, respectively. While the functional flood-plain is exposed to direct flooding, the fossil flood-plain is protected by dykes and only submerged by ascending groundwater.

The main objectives of the study were: (i) to assess the impact and relative importance of mowing on seedling recruitment and (ii) to explore the impact of other factors such as flooding regime, vegetation structure and environmental variation on seedling recruitment in alluvial meadows.

The results may provide useful information how different mowing regimes may support recruitment of sown or with plant litter transferred target species (Hölzel & Otte 2003) in restoration practice.

6.3 Material and methods

Study site

The study area is situated in the Holocene flood-plain of the northern Upper Rhine about 30 km southwest of Frankfurt, Germany (49° 40' N; 8° 25' E). The climate in this region is warm and dry with a mean annual temperature 10.3°C and a mean annual precipitation of 580 mm (Müller-Westermeier 1990). While winter, spring and early summer may bring floods, summers are often characterized by periods of drought. These climatic and hydrological conditions result in a high variability of soil water potential. The studied meadows occupy calcareous and extremely fine-grained alluvial soils with poor aeration and rapid hardening of the topsoil in dry periods.

In species-poor grassland two experimental sites were chosen, which differ with respect to their flooding regimes. One of the study sites is located in the functional flood-plain (FUN), between the river and the dyke and is directly flooded up to a height of 3 m. The other site, in the fossil flood-plain (FOS), situated in a depression on the landward site of the winter dyke, is submerged (< 1 m) exclusively by ascending, clear groundwater during high water levels of the Rhine. Both meadows are traditionally mown for haymaking in June and only in years of high precipitation a second cut is carried out in September.

Above-ground vegetation of both study sites was dominated by grasses such as *Alopecurus pratensis, Poa trivialis, Agrostis stolonifera* and *Elytrigia repens,* and at site FUN also by the forbs *Potentilla reptans* and *Symphytum officinale*. At the other meadow-site in the fossil flood-plain (FOS), also some ruderal forbs such as *Cirsium arvense* and *Polygonum amphibium* occurred.

Study species

We chose six long-lived perennial species that are characteristic of subcontinental flood-meadows of the alliance *Cnidion*. Two of these species, *Viola pumila* and *Iris spuria,* are extremely rare in Germany and Central Europe (Schnittler & Günther 1999) (Table 1). All plants predominantly recruit by seeds while clonal propagation is also possible (Klimeš et al. 1997) but of minor importance. Moreover, the selected species show considerable differences in seed mass (Table 1).

Table 1. Mean seed mass (mg), germination (%) under outdoor conditions and red list status of the selected flood meadow species.

	Seed mass [mg]	Germination rate [%]	Red list status
Galium wirtgenii	0.40	75	-
Inula salicina	0.16	77	-
Iris spuria	14.62	73	2
Serratula tinctoria	1.26	87	3
Silaum silaus	2.43	77	-
Viola pumila	1.08	84	2

Experimental design

In order to investigate the effects of different mowing regimes on recruitment of the six flood-meadow species, identical seed addition experiments were carried out at both sites. To asses the impact of mowing we used a split-plot design with four replicates. Each of the four blocks consisted of three randomized 2.30 x 4.20 m plots (main plots) where three different treatments were applied:

(i) mowing in May and August

(ii) mowing in Mid-June

(iii) mowing once in September (late mowing)

The two latter mowing treatments have typically been applied in the flood-meadows of the study area for approximately 20 years now. The treatment mowing in May and August was chosen to test the effects of an additional cut in the growing season.

The mowing in our experiment was carried out with a cutter bar mower of 1 m width. In all treatments the plant material was removed after mowing. Within each main plot, six subplots of 30 x 30 cm were established. In February 2002, 100 seeds of each species were sown into one of the subplots. The seeds had been collected in autumn 2001 in autochthonous populations of nearby flood-meadows. After collection, the seeds were cleaned and kept dry at room temperature.

Additionally, to assess outdoor germination rates under optimal conditions, two times 400 seeds of each species were sown in February 2002 into styrofoam trays filled with sterile soil and kept under outdoor conditions at an experimental field near Giessen. The trays were watered regularly and emerging seedlings were counted and removed. The study sites consisted of species-poor grassland with none of the sown species either in the above-ground vegetation nor in the seedbank. To test the latter we took soil seedbank samples of the

experimental sites in the year 2000. We analysed seedbanks with the seedling emergence method over 30 months (Roberts 1981).

To determine dry matter yield of biomass the standing crop of four randomly distributed plots (0.1 m²) were harvested at each cutting date and was dried at 60 °C for 48 hours and weighed afterwards. Cover of all higher plants, mosses, plant litter as well as the percentage of bare soil surface, was estimated visually three times a year. In each main plot we also determined photosynthetically active radiation (PAR, 400-700 nm) using a Line Quantum Sensor of one meter length (LI-COR: LI-191SA) at ground level and above the canopy.

The total number of seedlings in each plot was recorded in early summer, midsummer and autumn over two subsequent years.

Data analysis

To test for differences in treatments and species, Repeated-Measures analyses (ANOVA and MANOVA) for a split-plot design were applied. Prior to analysis, the data were log (x + 1) transformed to achieve normality and homogeneity of variances. In the Repeated-Measures ANOVA, the treatment and species were used as fixed effects, block as the random factor and time as the Repeated-Measures (within subject) factor. The effects of mowing were tested against its interactions with block and the species effects as well as its interactions, against the residual variance among the sub-plots. To test hypothesis about within-subject factors we used MANOVA, which is an alternative procedure that does not depend on the sphericity assumption and is therefore more appropriate for analyses of repeated measurements made on the same objects (Scheiner & Gurevitch 1993; Zar 1999). As test statistics of the MANOVA analysis we chose the robust Pillai's trace (Quinn & Keough 2002). For each site and date a separate univariate ANOVA was calculated. In case of significance ($p < 0.05$), the analysis was followed by a post-hoc Tukey's-Test. Repeated-Measures ANOVA, MANOVA and associated tests were calculated with SAS for Windows (Anon. 1999).

Correlations between the measured habitat variables and seedling numbers per treatment were analysed using Spearman rank correlation. These calculations were carried out with STATISTICA (Anon. 2002).

6.4 Results

Multivariate results of Repeated-Measures ANOVA showed for both study sites a significant treatment effect and highly significant species effects, however, the interaction between treatment and species was not significant (Table 2a). We furthermore detected a highly significant time effect and time x species interaction, indicating interspecific differences in germination phenology and seedling survival (Table 2b). For the study site in the functional flood-plain (FUN) univariate ANOVA showed a treatment effect in May 2003 whereas the species effect was significant in almost all cases (Table 3). The interaction between treatment and species was significant only once. With respect to the studied species in the functional flood-plain, the treatment effect revealed significance for *Galium verum* as well as for *Serratula tinctoria* (Table 4) and the time effect was significant only for *Iris spuria* which was probably due to the low number of germinated seedlings of the other study species. The weak treatment effects indicated that late mowing tended to be unfavourable for successful germination and establishment of seedlings (Fig. 1) which was also confirmed by the post hoc-test.

At the study site in the fossil flood-plain univariate statistics showed in the first year (2002) significant treatment and species effects as well as significant interaction effects between

Table 2. Multivariate results of Repeated-Measures ANOVA comparing effects of different mowing regimes on seedling recruitment at a meadow site in the functional (FUN) and fossil (FOS) flood-plain. The effects of between-subject factors were tested in an analysis of variance across all observations (a.), while MANOVA was used to test the within-subject-factor (time) and its interactions (b.). Abbreviations: df, degrees of freedom; MS, mean sum of squares; F, variance ratio. Significant *p*-values are given in bold.

a. Between-subject factors

	FUN				FOS			
	df	**MS**	**F**	***p***	**df**	**MS**	**F**	***p***
treatment	2	0.81	5.54	**0.043**	2	0.61	7.86	**0.021**
species	5	1.45	9.57	**<0.001**	5	1.22	9.78	**<0.001**
treatment*species	10	0.17	1.14	0.358	10	0.25	2.00	0.057
Error	45	0.15			45	0.12		

b. Within-subject factors

	FUN			FOS		
	Pillai's trace	**F**	***p***	**Pillai's trace**	**F**	***p***
time	0.5258	9.09	**<0.001**	0.4036	12.12	**<0.001**
time*treatment	1.8473	7.26	**0.012**	1.4596	1.62	0.287
time*species	1.7118	4.69	**<0.001**	1.9041	5.54	**<0.001**
time*treatment*species	0.8117	0.87	0.713	1.2242	1.46	**0.035**

them (Table 3). In contrast, in 2003 we found no significant treatment or interaction effects whereas the species effect was consistently significant. In line with this finding, the biomass production showed considerable differences between the two study years with an extremely low biomass production in the year 2003 at both study sites (Fig. 2). On the species level significant treatment effects were detected for *Inula salicina* and *Serratula tinctoria* whereas for *Viola pumila* the time x treatment effect was significant confirming that treatment effects changed over time (Table 4). In case of significant treatment effects, mowing in May and August revealed a higher number of observed seedlings suggesting a facilitation of recruitment by mowing twice a year.

The mean number of seedlings found on a single date of observation was highest at both sites for the large-seeded *Iris spuria.* In contrast, the lowest number of seedlings was shown by the small-seeded *Inula salicina,* which became already extinct in the fossil flood-plain in spring 2003. Since our control experiments under outdoor conditions showed a mean germination rate of 77 % for *Inula salicina,* which was the highest of all involved species (Table 1), the low recruitment success cannot be explained by a poor germinability of this species.

Interspecific differences in germination phenology were also found. In most species the bulk of seedlings emerged in the first spring (2002), whereas *Silaum silaus* and *Viola pumila* predominantly germinated a year later in spring 2003. *Iris spuria,* the monocotyledonous plant germinated at site FOS in autumn and at the other site (FUN) in spring 2003, indicating that germination was site specific (Fig. 1). Generally, the observed number of seedlings changed considerably over time. We also observed high mortality rates in some species, e.g. for *Iris spuria* and *Serratula tinctoria* in the fossil flood-plain (Fig. 1).

Additionally, none of the studied habitat variables (percentage of bare soil, percentage of vegetation cover, relative light intensity) was significantly correlated with the number of seedlings per treatment.

Generally, our experiments resulted in low final establishment rates for all species at both study sites (mostly < 7%) and weak treatment effects.

Table 3. Univariate results of ANOVA comparing effects of different mowing regimes on seedling recruitment on a meadow in the functional (FUN) and fossil flood-plain (FOS). For each site and date a separate ANOVA was calculated. Significant *p*-values are given in bold.

		Jun 02	**Aug 02**	**Okt 02**	**May 03**	**Jul 03**	**Sep 03**
FUN	treatment	0.178	0.064	0.104	**0.048**	0.280	0.205
	species	0.064	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	treatment*species	0.545	0.537	**0.045**	0.485	0.541	0.574
FOS	treatment	**0.022**	**0.014**	**0.001**	0.739	0.244	0.331
	species	**0.030**	**<0.001**	**<0.001**	**<.001**	**<.001**	**<.001**
	treatment*species	**0.029**	**0.012**	**0.009**	0.160	0.694	0.836

Table 4. Univariate results of Repeated-Measures ANOVA comparing effects of different mowing regimes on seedling recruitment. For each site and species a separate Repeated-Measures ANOVA was calculated. MANOVA was used to test the within-subject-factor (time). For full species names see Table 1. Significant *p*-values are given in bold.

		Gal wir	**Iri spu**	**Inu sal**	**Vio pum**	**Sil sil**	**Ser tin**
FUN	treatment	**0.050**	0.514	0.690	0.177	0.571	**0.010**
	time	0.147	**0.016**	0.488	0.685	0.264	0.420
	time*treatment	0.837	0.331	0.719	0.691	0.606	0.793
FOS	treatment	0.282	0.198	**0.007**	0.220	0.362	**0.014**
	time	**0.008**	**0.002**	0.083	0.054	0.103	**0.012**
	time*treatment	0.555	0.232	0.321	**0.022**	0.416	0.071

6.5 Discussion

At the end of the second year establishment rates of less than 7 % of available seeds for the six flood-meadow species demonstrated a lack of suitable microsites in both study sites and all management regimes. The low establishment rates are in line with other field studies in moist grasslands (Bakker 1989; Kotorová & Lepš 1999) and are in particular comparable with experiments from dry calcareous grasslands (Silvertown & Dickie 1981; Kupferschmid et al. 2000). Germination rates in the field were considerably lower than under controlled outdoor conditions (Table 1) which was also found by e.g. Kotorová & Lepš (1999) and Isselstein et al. (2002).

Generally we found weak treatment effects of mowing on final seedling establishment. Similar results for grasslands were reported in some other studies (Meyer & Schmid 1999; Coulson et. al. 2001). MANOVA showed no significant treatment x species interaction at both study sites and species identity seemed to be the major factor influencing variance in recruitment. However, univariate ANOVA revealed at the study site in the fossil flood-plain significant treatment x species interactions in the first study year whereas in the second year no significant effects of mowing were detected. This indicated that effects of mowing changed over years, which is also expressed in Table 2 as a significant time x treatment x species interaction. The results confirmed that in the first study year mowing in May and August facilitated seedling recruitment (e.g. *Serratula tinctoria*, Fig. 1) by lowering the high amount of above-ground biomass. Mowing two times reduced competitive effects with established plants and led to a subsequent higher incidence of light for seedling establishment (Jutila & Grace 2002). Similar, positive effects of mowing in early phases of seedling recruitment in wet grasslands were found by Bakker et al. (1980), Kotorová & Lepš (1999) and Jensen & Meyer (2001).

In spring 2002/2003 a high number of seedlings died in the fossil flood-plain due to a long lasting flooding event and the few survivors as well as the newly germinated seedlings showed no longer a significant mowing effect in 2003. Probably, in this year, which is characterized by an extremely low biomass production, the effects of mowing were largely overruled by the severity of summer drought.

The establishment rates showed considerable differences among species (Fenner 1978; Kotorová & Lepš 1999). While the highest number of germinated seeds was found in the large-seeded *Iris spuria*, the small-seeded *Inula salicina* showed extremely low germination

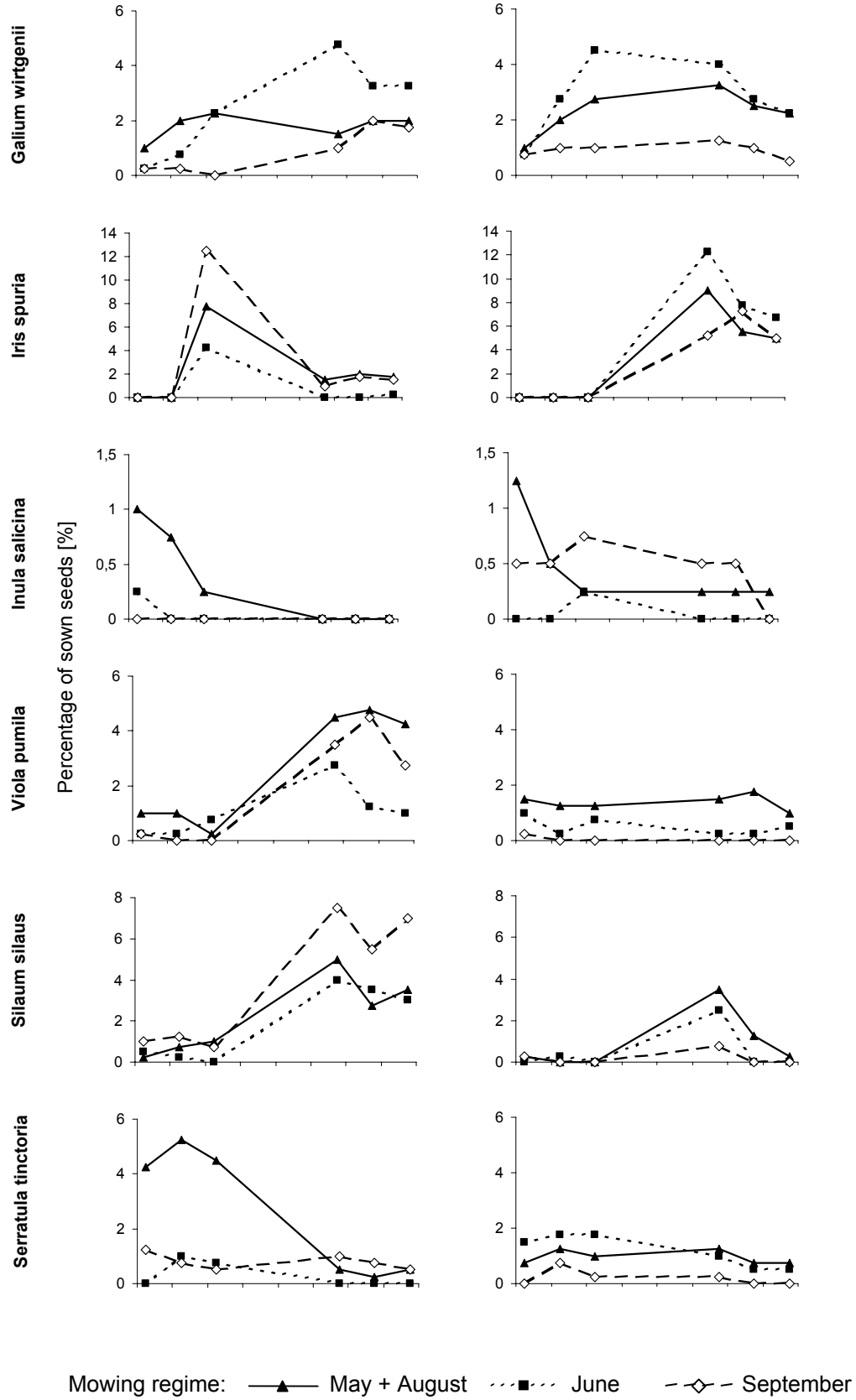

Fig. 1. Effects of mowing treatments on seedling recruitment of six flood-meadow species in the fossil (FOS) and functional (FUN) floodplain.

rates and in some plots a complete failure of germination. These results confirmed that small-seeded species are generally more sensitive to gap characteristics (Gross 1984) while large-seeded ones show high rates of seedling establishment in grasslands (Moles & Westoby 2002). This is because seedlings from large-seeded species are more tolerant towards competition by established vegetation (Bakker 1989; Ryser 1993; Jakobsson & Eriksson 2000) and physical hazards such as drought (Leishman et al. 2000). Germination phenology was species-specific although most species germinated in spring. E.g. in *Silaum silaus* highest germination rates occurred only in the second spring. *Iris spuria*, even showed site specific germination patterns: As found in earlier studies this species germinates at site FOS predominantly in late summer (Hölzel & Otte 2004a) of the first year, but at site FUN germination started as late as spring of the second year. This clearly shows that the onset of germination depend on site-specific environmental conditions, in particular on a suitable moisture supply.

The low recruitment success might be explained by the severity of drought in spring and summer 2003 which also led to desiccation and rapid hardening of the topsoil and thus negatively affected seedling survivorship (Ryser 1993; Stampfli & Zeiter 1999). Additionally to other studies (Oomes & Elberse 1976; De Jong & Klinkhamer 1988; Riba et al. 2002), our results suggest that soil moisture conditions are a crucial factor controlling germination and seedling survival, particularly in flood-meadows. The more unbalanced moisture regime (poor water supply in summer) in the functional flood-plain combined with extreme summer drought might be the reason for the high summer mortality rates of e.g. *Silaum silaus* or *Iris spuria*. As the biomass production at this site was nearly threefold higher in 2002 than in 2003, it indicates that competitive effects of the surrounding vegetation on seedling

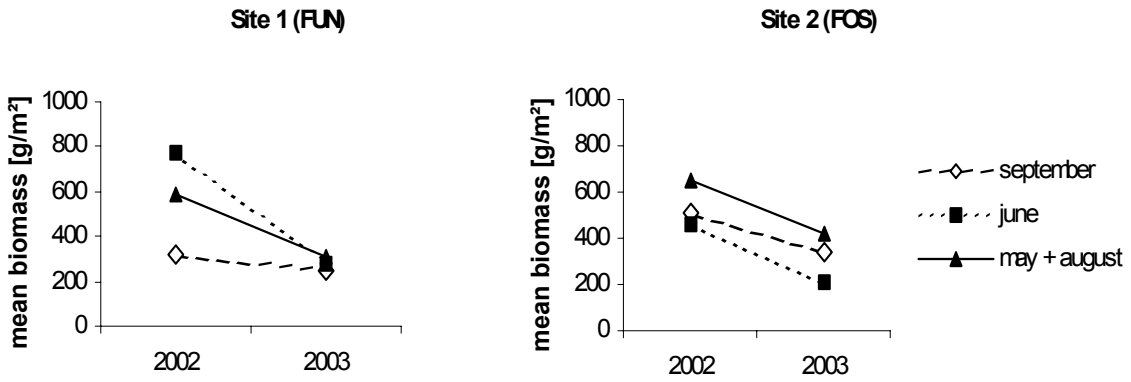

Fig. 2. Mean biomass production of the two study sites in the fossil (FOS) and functional (FUN) flood-plain with respect to different mowing treatments in 2002 and 2003.

recruitment played only a minor role in 2003. Seedling mortality due to long lasting flooding events in winter or spring had also a strong effect on establishment rates, which is clearly shown by the considerable decrease of *Iris spuria* and *Serratula tinctoria* after an inundation in spring 2003 in the fossil flood-plain. However, such flood disturbances often also remove the above-ground vegetation and create establishment opportunities for seedlings. Thus, the open canopy structure and the constant and relatively high moisture supply after the flood in spring 2003 may be the reason for the high germination rate of *Viola pumila* and *Silaum silaus* in the fossil flood-plain. It seemed that in our study plots temporal variation in annual climate and the resulting variation in hydrological conditions had a strong effect on seedling germination and establishment (Kellogg et al. 2003), independent of disturbances such as mowing. This is confirmed by Hölzel (accepted) who found much higher establishment rates in similar experiments 2001 at the same study site due to more favourable soil moisture conditions.

The lack of significant correlations between measured environmental variables and seedlings per treatment also indicated that extreme events like flooding and drought have a higher influence on successful recruitment than the vegetation structure of the sward itself.

In addition, we observed that the seedlings could persist without apparently making any growth during the two study years, which was also observed by Fenner (1978) for a few grassland species (e.g. *Rumex acetosa*). After two years none of the sown seedlings reached the stage of a flowering generative adult. Seedlings in these alluvial grasslands obviously only spend energy for growth in case of suitable environmental conditions, in particular soil moisture conditions.

Conclusions

Beyond the minor effects of the applied treatments, natural events such as flooding and drought appear to be crucial factors in determining the rate of germination and establishment. Our results suggest that the high spatio-temporal variability of site conditions in flood-plains induce occasionally occurring events of successful recruitment whereas in other cases establishment may be poor or even completely fail. This also means that restoration measures aiming at the reintroduction of target species by sowing or plant material transfer may require temporal replication to ensure success.

Despite the predominance of other environmental impacts in our particular case the obtained results also suggest that mowing two times a year at sites with high biomass production will increase establishment rates (Bakker et al. 1980; Jones & Hayes 1999).

Acknowledgements

We are grateful to Josef Scholz-vom Hofe and Christiane Lenz-Kuhl for their assistance in field work and in mowing the experimental sites. We also would like to thank Lutz Eckstein for valuable comments on the manuscript. This study was funded by the German Federal Agency for Nature Conservation.

7 Population structure of the threatened perennial *Serratula tinctoria* in relation to vegetation and management

Stephanie Bissels, Norbert Hölzel & Annette Otte

Applied Vegetation Science 7: 267-274

7.1 Abstract

Question: How does vegetation and management affect the population stage structure of *Serratula tinctoria*, a species indicative of highly endangered and species-rich flood-plain meadows? Are different management regimes suitable to support viable populations of *S. tinctoria*?

Location: Flood-plain of the northern Upper Rhine, Germany.

Methods: We analysed the population structure of *S. tinctoria* at 24 meadow sites which differed in vegetation and management. In this comparative study the investigated meadows were either (i) late mown in September, (ii) early mown in June or (iii) mown in June and then grazed by sheep.

Results: The structure of the surrounding vegetation had a clear effect on the population structure of *S. tinctoria*. The percentage of bare soil as well as the cover of bryophytes were positively related, whereas the Ellenberg N value of the established vegetation was negatively related to the density and proportion of seedlings. Generally, we found only slight differences between the population structure of *S. tinctoria* in early and late mown meadows. Both management regimes had high densities of seedlings. In contrast, the meadow pastures supported significantly lower densities of seedlings and generative adults but relatively high densities of juveniles and vegetative adults, indicating a higher importance of clonal propagation under grazing pressure.

Conclusions: Our results clearly showed that viable populations of *S. tinctoria* may occur in all of the studied management regimes. Although *S. tinctoria* was considered to be highly sensitive to early mowing, our findings suggest a facilitation of the species by mowing in June at more nutrient-rich sites, which is also a benefit for the integration of management in farming systems.

Keywords: Conservation; Demography; Flood-plain meadow; Grazing; Long-lived perennial; Mowing; Recruitment.

7.2 Introduction

The persistence of many plant species in semi-natural grasslands depends on a regular and appropriate management. Mowing and grazing are important factors for the maintenance and restoration of high species richness in grasslands (Bakker 1989; Güsewell et al. 2000; Grime 2002). Management regimes have a major impact on the availability of seeds and of suitable safe sites (Harper 1977), which are key factors for reproduction and successful recruitment in plant populations (Eriksson & Ehrlén 1992). Grazing is known to create gaps in the sward that facilitate seedling recruitment (Watt & Gibson 1988; Bullock et al. 1994), whereas mowing can prevent asymmetric light competition (Lepš 1999) but may also hamper seed production (Coulson et al. 2001). Additionally, grassland species are characterized by different mowing and grazing compatibilities, which may be affected by livestock feeding preference and the capacity for regeneration after disturbance (Briemle et al. 2002).

These examples indicate that management regimes can differently affect the dynamics and composition of plant communities and individual plant species. Therefore, the investigation of plant population dynamics in relation to management and environmental variation is of major interest in the successful conservation of threatened plant species. Traditional management regimes often contradict the demands of modern agriculture. In particular, it is difficult to incorporate biomass from late mown meadows in existing farming systems without high compensation payments. Consequently, there is often an urgent need to assess the suitability of alternative management options in maintaining target communities (Bühler & Schmid 2001; Hegland et al. 2001).

The analysis of life stages of perennial plants can provide information for the improvement of conservation and management strategies (Oostermeijer et al. 1994). In contrast to detailed individual-based demographic investigations, the analysis of the population stage structure is less laborious, which has the advantage of better representation since more replicates can be sampled. Although only a single census per population is conducted, several studies confirmed the usefulness and appropriateness of this method (Oostermeijer et al. 1994; Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002). In the present study we used this approach to assess the suitability of different management regimes for the preservation of highly endangered species-rich flood-meadows along the northern Upper Rhine in Germany. The perennial herb *Serratula tinctoria,* characteristic of species-rich flood-meadows (Hölzel 1999), was chosen as a model species. We studied the demographic

structure of this species in 24 populations with respect to management, site conditions and vegetation.

The main objectives of the study were (i) to assess the impact of site conditions, vegetation structure and species composition on population stage structure and (ii) to evaluate management options for the sustainable conservation of *S. tinctoria* populations and species-rich flood-meadows in general.

7.3 Methods

Study species

Serratula tinctoria is a long-lived herbaceous perennial plant, which predominantly occurs in fen meadows and alluvial grasslands on base-rich soils, but also in open deciduous forests, along forest edges and in heathlands (Hegi 1987). The species is considered to be a character species of late mown nutrient-poor *Molinion* grasslands (Oberdorfer 1983). In our study area and in other parts of Central Europe *S. tinctoria* occurs widely in more nutrient-rich flood-meadows of the alliance *Cnidion* (Burkart 1998; Hölzel 1999), which were traditionally used for haymaking. These meadows are characterized by a high variability in soil water potential. While winter, spring and early summer may bring floods, summers are often characterized by periods of drought. *S. tinctoria* is known as a species particularly well adapted to highly variable soil moisture conditions.

Germination of the relatively large seeds occurs in autumn directly after shedding or in the next spring (Hölzel & Otte 2004a) and there is no indication of a long-term persistent seed bank (Hölzel & Otte 2004b). This iteroparous species flowers from July until October. The flowers are pollinated by various insects (*Hymenoptera, Diptera, Lepidoptera*) and the diaspores are adapted to wind dispersal (Müller-Schneider 1986, Bischoff 2002). *S. tinctoria* can also propagate clonally by forming daughter rosettes at the end of short stolons (Klimeš et al. 1997).

Due to the Central European core area of the species, Germany has a high responsibility for the worldwide preservation of *S. tinctoria* (Welk 2002).

Study area and Sampling

In the Hessian portion of the Holocene flood-plain of the northern Upper Rhine between the tributaries Neckar to the south and Main to the north, 24 study sites in flood-meadows were selected. The investigated meadows are subject to the following management regimes:

1. Mowing once in September (late mowing) (n = 8).
2. Mid-June mowing (early mowing). These meadows were used for haymaking and only in years of high precipitation is a second cut conducted (n = 9).
3. Meadow mown in June and grazed in late summer or autumn by a free-ranging flock of sheep (n = 7).

All sites are in nature reserves and the current management regimes have been applied for ca. 20 years.

In August and September 2002, in each population, two randomly selected 1 m² plots (in one population just one plot) were analysed, yielding a total of 47 samples. The total number of individuals in each plot was counted. Although clonal propagation was also possible, each rosette was considered as an individual. For the classification of life stage classes in each individual the total height, total length of the longest leaf, length and width of the longest leaf blade and the number of leaves per rosette were measured. In generative plants the number of flowerheads and stalks was also counted.

To describe species composition the abundance of all vascular plant species was estimated using a modified Braun-Blanquet scale (van der Maarel 1979). We estimated total vegetation cover, the coverage of mosses, plant litter, the percentage of bare soil surface and mean vegetation height as indicators of vegetation structure. Light intensity penetrating to the ground was measured using a 1-m long Line Quantum Sensor (LI-COR: LI-191SA). We recorded photosynthetically active radiation (PAR, 400-700 nm) simultaneously at ground level and in full light above the canopy. Light penetration was expressed as percentage of the latter value. Light measurements were performed in August and were repeated four times at random in each plot. To determine population size, we counted all flowering plants in small populations. In large populations (>500 individuals) we used the mean number of reproductive plants per m² and extrapolated it to a value for the total population area. The number of flowering plants per population ranged between 25 and 5000.

Classification of life stages

Based on our field observations of 7055 individuals we distinguished four different life stages, which were defined by leaf number, leaf size and the presence or absence of flowers. To evaluate the appropriateness of the chosen classification and to clarify critical cases we also applied the method of *k*-means clustering (Legendre & Legendre 1998). The final life stage classes were defined as follows:

1. Seedlings (s) had cotyledons and up to three primary leaves (maximum length of the longest leaf 10 cm, mean length of leaf blade 1.7 cm).
2. Juveniles (j) had mostly four leaves with a maximum length of the longest leaf of 20 cm.
3. Vegetative adults (vA) were characterized by a rosette with between 5 and 11 leaves. The leaves were coarsely serrate, more solid and the texture was more structured than the leaves of the juveniles.

4. Generative adults (gA) normally had one, and in the early mown meadows up to four, flowering stalks. Rosettes whose flowering stalks had been grazed were also considered as generative adults.

Data analysis

For each population the density per m² and the relative proportion of the different life stage classes was calculated.

To assess compositional gradients in the vegetation of the study plots we used Detrended Correspondence Analysis (DCA) on square root transformed cover data (species with less than three occurrences were excluded). Axis 1 had a gradient length of 3.023 standard deviation units and thus showed some unimodality (Legendre & Legendre 1998; Ter Braak & Šmilauer 1998). The vegetation data were also used to calculate cover weighted means of the Ellenberg indicator values for moisture, light and nutrients (Ellenberg et al. 1992). Correlations between axes scores and habitat variables were analysed using the Pearson correlation coefficient.

The relationship between habitat variables and the density or proportion of each life stage was investigated by simple and multiple regression analysis. Spearman rank correlation coefficients between predictor variables were examined to detect collinearity (Quinn & Keough 2002). Intercorrelated variables were omitted, which resulted in four remaining habitat variables (cover of bryophytes, open soil, relative light intensity, Ellenberg N) and these were chosen as predictor variables in the multiple regression model. We applied the more robust stepwise backward selection procedure (Zar 1999). Proportions were angular transformed and the remaining predictor variables square root transformed prior to regression analyses to meet the normality assumption.

To analyse the counts of individuals per plot and to test for differences in the demographic status of *S. tinctoria* between management regimes, we conducted univariate two-way ANOVA with the densities of each life stage as dependent variable and management type as well as population as factors. Population was used as a nested random factor within the management regimes. In one population only one plot was analysed so we omitted this population from the analysis, yielding 23 populations in total. To test for the overall effect of management and population we applied a MANOVA. Out of the four common MANOVA statistics we chose the recommended more robust Pillai's trace for interpretation of results (Quinn & Keough 2002). Prior to analysis the frequencies were log-transformed (x + 1) and we achieved normally distributed residuals and homogeneous variances. In case of

significance, the analysis was followed by a Tukey's test for unequal sample sizes. The differences in number of flowerheads between management regimes were also analysed by two-way ANOVA and followed by a Tukey's test.

Detrended Correspondence Analysis ordination was performed using the software package PC-ORD 4.14 (McCune & Mefford 1999). Regression analyses was carried out with the General Linear Model module of STATISTICA 6.0 (Anon. 2002). ANOVA, MANOVA and associated tests were calculated with SAS for Windows (Anon. 1999).

7.4 Results

Comparison of species composition and site variables

The DCA-ordination revealed a clear floristic gradient between early and late mown meadows with *S. tinctoria*. Whereas late mown stands had a high floristic variation along the first axis, early mown meadows and the meadow pastures were more uniform, which is indicated by a clumped distribution in the lower left corner of the ordination graph (Fig. 1).

The first axis showed a positive correlation with the Ellenberg indicator value for light ($r = 0.62$, $P < 0.05$) and a negative correlation with the Ellenberg nutrient value ($r = -0.54$, $P < 0.05$) and the percentage of vegetation cover ($r = -0.50$, $P < 0.05$). The second axis displayed a positive correlation with vegetation height ($r = 0.48$, $P < 0.05$). All other variables were not significantly correlated with the DCA axes.

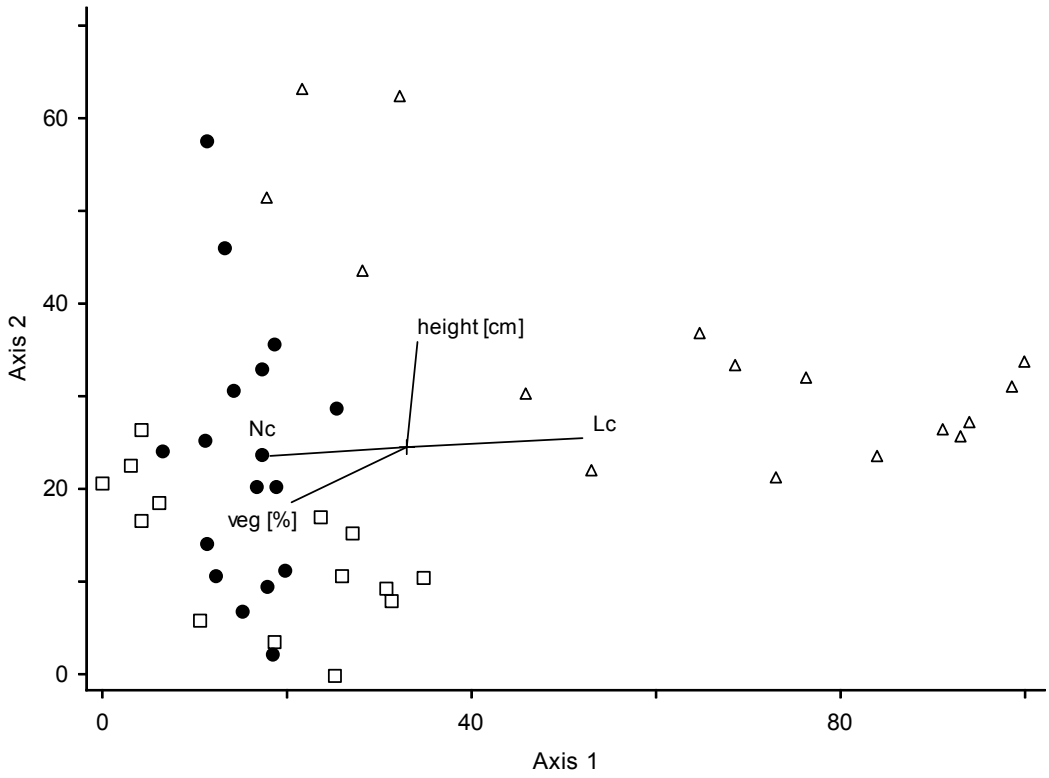

Fig. 1. Jointplot based on Detrended Correspondence Analysis of 47 plots in differently managed meadows with respect to site variables. Triangles = late mown meadows; circles = early mown meadows; squares = meadow pastures; L_c = Ellenberg indicator value for light; N_c = Ellenberg indicator value for nitrogen; height (cm) = measured canopy height; veg (%) = percentage cover of the vegetation.

Relationships between vegetation structure, species composition and population structure

Multiple regression analyses confirmed a clear relationship between the structure and floristic composition of the surrounding vegetation and some life stage classes of the studied populations. In the regression model the cover of bryophytes and the percentage of bare soil were positively correlated with seedling density, whereas the Ellenberg nutrient value was negatively correlated with seedling density (Table 1). Similarly, in the proportion of seedlings a large part of variance (52%) was explained by habitat variables. Besides the above-mentioned variables, relative light intensity was additionally retained as significant predictor of the proportion of seedlings. Furthermore, the density of generative adults also showed a positive correlation with the cover of bryophytes and a negative correlation with the Ellenberg nutrient value. Conversely, the proportion of vegetative adults was negatively correlated with the cover of bryophytes and the percentage of open soil and positively with the Ellenberg nutrient value.

Table 1. Stepwise multiple regression of the relationship between the density or proportion of four life stage classes of *Serratula tinctoria* and habitat characteristics on the population level (n = 24). For the full model four predictor variables were chosen (see text). Backward selection of variables was used ($P < 0.05$) [R^2 = adjusted coefficient of determination, β = standardized regression coefficient, t = t-test for the deviation of β from zero].

	Predictor variable		β	t	P
a. Densities					
Seedlings (ind./m²)		R^2= 0.326			
	Cover bryophytes (%)		0.461	2.421	0.025
	Open soil (%)		0.572	2.921	0.008
	Ellenberg N		-0.427	-2.394	0.027
Generative adults (ind./m²)		R^2= 0.316			
	Cover bryophytes (%)		0.367	2.105	0.047
	Ellenberg N		-0.439	-2.520	0.020
b. Proportion of plants					
Seedlings (%)		R^2= 0.522			
	Cover bryophytes (%)		0.664	3.906	< .001
	Open soil (%)		0.709	4.214	< .001
	Light (%)		0.364	2.336	0.031
	Ellenberg N		-0.364	-2.381	0.028
Vegetative adults (%)		R^2= 0.454			
	Cover bryophytes (%)		-0.452	-2.639	0.016
	Open soil (%)		-0.589	-3.335	0.003
	Ellenberg N		0.561	3.497	0.002

We also found significant positive correlations of the density and the proportion of seedlings with the estimated population size (R^2 = 0.390, df 22, P <0.001; R^2 = 0.357, df 22, P = 0.001).

Impact of management on population structure

Univariate two-way ANOVA of the mean density of *S. tinctoria* life stages revealed significant differences between management regimes for the seedling and generative adult stage class (Table 2). Significant differences between the density of populations were found in all life stage classes with the exception of the vegetative adults. Despite these high variability between populations (Pillai's Trace < .0001), MANOVA of all life stage classes resulted in an overall significant management effect (Pillai's Trace 0.0003).

As shown in Fig. 2 the density of seedlings and generative adults significantly differed between management regimes while juveniles and vegetative adults showed no differences in their densities. The *post-hoc* test confirmed that the meadow pastures had significantly lower densities of seedlings than the late or early mown meadows (Fig. 2). Similarly, the mean density of generative adults was also significantly higher in early and late mown meadows than in meadow pastures. Generally, there were only slight differences between early and late mown meadows, whereas the meadow pastures were characterized by a divergent population structure. Although the meadow pastures had a lower density of seedlings and generative adults, the density of juveniles was comparable and the density of vegetative adults was even slightly higher than in the other management regimes.

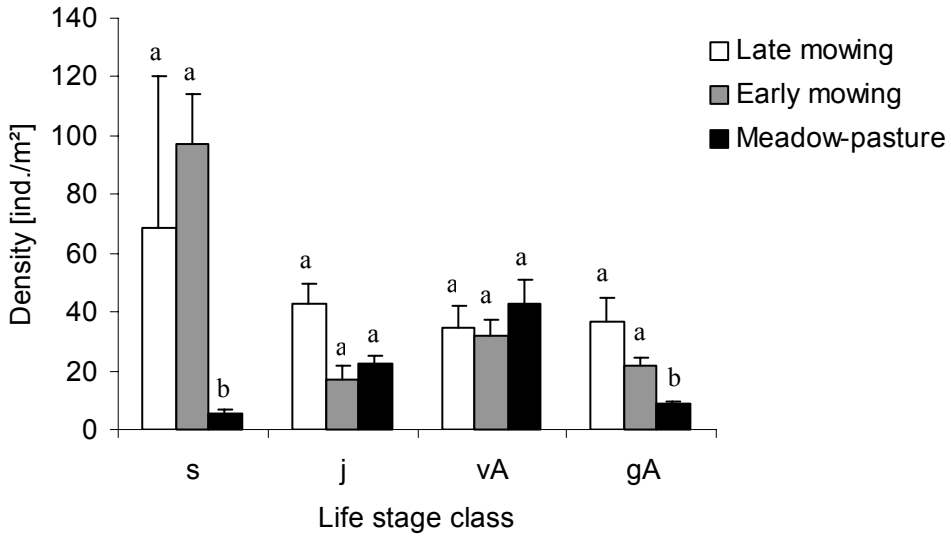

Fig. 2. Mean densities of life stage classes of 24 populations of *Serratula tinctoria* with respect to different management regimes. Letters indicate if means differ significantly in life stage class at α < 0.05 (Tukey's-Test). [s = seedlings, j = juveniles, vA = vegetative adult, gA = generative adult].

The number of flowerheads per population was significantly higher in both late and early mown meadows than in meadow pastures (Fig. 3). The same was true for the mean number of flowerheads per plant and population, which was significantly higher in early mown meadows than in meadow pastures ($\alpha = 0.05$, Tukey's test).

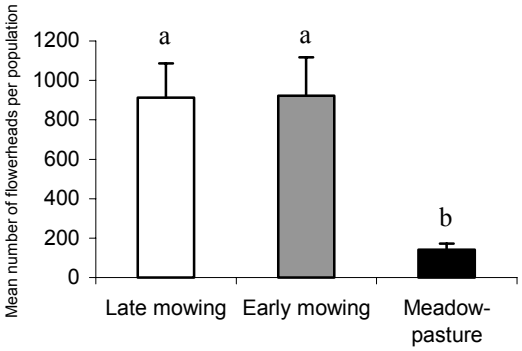

Fig. 3. Mean number of flowerheads per population of *Serratula tinctoria* and standard error with respect to three different management regimes. Letters indicate if means differ significantly at $\alpha < 0.05$ (Tukey's test).

7.5 Discussion

Effects of habitat conditions on population structure

The structure and composition of the surrounding vegetation showed a strong effect on the population structure of *Serratula tinctoria*. For seedlings, the main variables of influence were cover of bryophytes, open soil and Ellenberg N-value. The percentage of bare soil was positively correlated with the density and proportion of seedlings, which confirms earlier evidence that gaps provide particularly suitable conditions for germination and seedling recruitment in grasslands (Grubb 1977; Silvertown 1981; Krenová & Lepš 1996; Kotorová & Lepš 1999).

The positive relationship between cover of bryophytes and density or proportion of seedlings may be interpreted as a protective effect of the moss layer on seed germination. These results agree with findings of Ryser (1993) and Oostermeijer et al. (1994). The latter hypothesized that the moss layer reduces winter mortality of seedlings. The bryophyte layer may also provide protection against seed predation (Van Tooren 1988) or prevent desiccation of seedlings (Špačková et al. 1998). During & van Tooren (1990) emphasized that the protective role of the moss layer is more important in communities with high summer drought or temporal desiccation, which is in line with the environmental situation in the studied flood-meadows. In contrast, several authors found inhibiting effects of the bryophyte layer on seedling recruitment in permanently wet meadows (Špačková et al. 1998; Kotorová & Lepš 1999; Eckstein et al. 2004).

Table 2. Univariate two-way ANOVA of the density of life stage classes of 23 *Serratula tinctoria* populations in three management regimes. Population was used as a nested random factor within the management regimes. Prior to analysis the frequencies were log-transformed (x + 1) [MS = mean squares].

	Source of variation	df	MS	F	*P*
Seedlings	Management	2	4.208	6.41	0.007
	Population (Management)	20	0.656	9.17	<.001
	Error	23	0.072		
Juveniles	Management	2	0.249	0.70	0.507
	Population (Management)	20	0.354	2.09	0.046
	Error	23	0.170		
Vegetative Adults	Management	2	0.095	0.68	0.518
	Population (Management)	20	0.139	0.87	0.622
	Error	23	0.160		
Generative Adults	Management	2	1.491	7.96	0.003
	Population (Management)	20	0.187	5.99	<.001
	Error	23	0.031		

Higher nutrient availability indicated by Ellenberg nutrient values also led to a decrease in the number and proportion of *S. tinctoria* seedlings which corresponds with the findings of Rusch & Fernandéz-Palacios (1995) and Lepš (1999). Similarly, the percentage of light reaching the soil surface was positively related to the proportion of *S. tinctoria* seedlings, which was also found by other authors as a major factor controlling recruitment (Jensen & Meyer 2001; Jutila & Grace 2002).

In contrast vegetative adults were negatively related to the cover of bryophytes and open soil and positively correlated with the Ellenberg nutrient value. This showed that vegetative adults predominantly occurred in habitats with different vegetation structure and floristic composition than seedlings. As confirmed by the other results (Fig. 2) the more nutrient-rich meadow pastures are characterized by high densities of vegetative adults.

Effects of late and early mowing

As shown in Fig. 3, viable populations of *S. tinctoria*, suggested by high numbers of seedlings, occurred in early as well as in late mown meadows. The mean density of seedlings in early mown meadows was even higher than in late mown meadows. This indicated, that although these meadows were cut in June, germination and early establishment were successful. The rosette species *S. tinctoria* rarely flowered before mid-June and was able to recover rapidly after cutting, which is a general character of many rosette species (Briemle & Ellenberg 1994). Even if the plant already had a stem with buds it responded to cutting by a rapid re-growth of two or more generative stems (personal observation). Similar results were obtained by Lennartsson and Ostermeijer (2001) who showed that *Gentianella campestris* had a high capacity for compensatory seed production after mid-July mowing. After mowing in June, *S. tinctoria* flowers from early August onwards and sets seeds in September or October. This also applies to other target-species of flood-meadows, such as *Sanguisorba officinalis, Silaum silaus*, *Inula salicina*, *Allium angulosum* and *Cnidium dubium* (Joyce 1998; Hölzel et al. 2002). These species may benefit from competitive release after hay-making in early June inducing a higher availability of light. For flood-meadows along the Elbe River, Leyer (2002) found that early mowing prevent species-rich stands forming a dense litter layer and weakens competitors with predominantly vegetative propagation such as *Elymus repens* or *Phalaris arundinacea.*

Our results clearly suggest a facilitation of *S. tincoria* by early mowing in relatively nutrient-rich *Cnidion* meadows. This contrasts with other authors who have reported sensitivity to early mowing (Briemle & Ellenberg 1994, Briemle et al. 2002). However, in the case of early

mowing no, or a very late, second cut in autumn appears to be of crucial importance. An early second cut in August or September, would probably lead to a failure of seed production due to immature seeds at the time of mowing (Hölzel 1999) and thus negatively affect the viability of *S. tinctoria* populations in the long-term. As pointed out in many other studies (e.g. Hegland et al. 2001; Overbeck et al. 2003) management regimes have to respect the phenology of seed production to assure the potential for dispersal and non-clonal regeneration.

Effects of grazing

In contrast to early or late mown populations, the meadow pastures were characterized by low densities of seedlings and generative adults, but relatively high densities of juveniles and vegetative adults. The low number of seedlings is most likely an effect of the damage to adult plants and their seeds by subsequent grazing, which reduces the potential for the recruitment of new individuals (Bastrenta 1991; Bühler & Schmid 2001; Lennartsson & Oostermeijer 2001). This is also illustrated by a significantly lower number of flowerheads in the meadow pastures. As indicated by the relatively high proportion of vegetative adults, the reduced generative reproduction under grazing pressure seems to be at least partly compensated by a raised importance of clonal propagation.

More suitable conditions for establishment of *S. tinctoria* in the meadow pastures due to trampled gaps (Bullock et al. 1995; Lennartsson & Oostermeijer 2001) were not detected, which was also reported for coastal grasslands by Jutila (2003). In contrast, mowing alone creates moderate sward disturbance through hay-making machinery (Bakker et al. 1980) which provides a sufficiently high number of regeneration niches, which is quite often found in relatively large-seeded meadow species (Kotorová & Lepš 1999).

Based on the results of the DCA ordination (Fig. 1) one may at first argue that the effects of different management regimes are a result of differences in site conditions indicated by the nutrient gradient along the first axis, which separates early mown meadows and meadow pastures on the one hand from late mown meadows on the other. However, contrary to this expectation, major differences in stage structure were not found between late and early mown meadows but between these two and meadow pastures. The overall significance of management effects could also be confirmed by MANOVA.

Conclusions

Our results clearly showed that viable populations of *S. tinctoria* may occur in early as well as in late mown meadows and even in meadow pastures, which have received this type of management for more than 20 years. Contrary to traditional beliefs, there is no urgent need for late mowing, which considerably widens the options of agricultural use. Hay from early mown flood-meadows may be easily incorporated as basic fodder in feeding systems for cattle and horses (Donath et al. 2004). In accordance with other studies, our results suggest that the analysis of population structure of long-lived perennials such as *S. tinctoria* is a particularly useful tool to evaluate the suitability of different management options for the preservation of endangered semi-natural grassland species (Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002).

Acknowledgements

We are grateful to Tobias W. Donath and Cigdem Özalp for their assistance in the field. We would also like to thank Lutz Eckstein and Tobias W. Donath for statistical advice and for critical reading the manuscript. H. Jutila, two anonymous referees and the co-ordinating editor made valuable comments on earlier drafts of the paper. This study was funded by the German Federal Agency for Nature Conservation.

8 General discussion

8.1 Ecological constraints in grassland restoration

The role of abiotic site conditions

The evaluation of previous restoration measures clearly showed that limited dispersal was the main obstacle in the restoration of highly endangered flood-plain communities along the northern Upper Rhine (chapter 4). After 15-20 years of restoration management the floristic structure of new meadows was still dominated by sown grasses and a high proportion of ruderal and arable species. Target species of flood-meadows largely failed to establish in both flood-plain compartments. The low restoration success cannot be explained by unsuitable abiotic site conditions, because old and new meadows differed only slightly in terms of soil nutrient properties and biomass yield. The organic matter content or the content of total nitrogen for example was even lower in the new meadows than in the species-rich old meadows within each compartment. Significant differences in plant available phosphorus and biomass yield were only found between flood-plain compartments. These differences may result from the later cessation of fertilizer application in the fossil flood-plain (1988 compared to 1983 in the functional flood-plain) or from a better moisture supply due to more constant and higher groundwater tables in the fossil flood-plain.

Generally, the relative importance of abiotic site conditions and the significance of a reduction of soil fertility for a successful restoration of target communities is not yet clarified. Many authors stated that a high soil fertility is a key factor limiting the increase in species diversity of many restoration grasslands after conversion from intensive agricultural management (Kapfer 1988; Oomes 1990; Marrs 1993). Various studies on the influence of nutrient availability on species richness in different grassland types indicate a dependency mainly on low phosphorus availability (Gough & Marrs 1990; Venterink et al. 2001) or low phosphorus availability in combination with low potassium availability (Oomes et al. 1996). In this context some authors point out that the depletion of nutrient availability for restoration purposes by cutting alone, particularly with regard to phosphorus, is a slow and uncertain process (Berendse et al. 1992; Tallowin et al. 1998). Janssens et al. (1998) suggested in a study concerning to the relation between soil chemical characteristics and plant diversity that on soils rich in organic matter, extractable P concentrations should not exceed 5 mg/100g soil ($\triangleq$ 11.45 mg P_2O_5 / 100g soil). Similar conclusions were drawn by Critchley (2002). However, in our study even species-rich old meadows in the fossil flood-plain showed much higher phosphorus contents, which indicated that soil nutrient concentrations are highly variable

within and between different grassland communities as well as in response to environmental variables such as management practices or climate. Hence, it remains unclear to what extent soil nutrient conditions or elevated phosphorus concentrations allow the development of species-rich communities in a particular habitat and how these may differ from local grassland reference sites.

A restoration measure to accelerate nutrient impoverishment and create favourable conditions for seedling recruitment is topsoil removal. In an experiment in our study area topsoil removal was revealed as a very effective method to reduce nutrient availability to the same level as species-rich reference sites (Hölzel 2003). Subsequent diaspore transfer with plant material on this restoration site was extremely successful. However, topsoil removal is a very crude measure and it is problematic to conduct it on a large scale. Thus another restoration project aiming at the re-establishment of species-rich alluvial grasslands on ex-arable soils with diaspore transfer by plant material but without top soil removal was initiated in 2000 (Hölzel & Harnisch 2002). First results show that re-establishment even on relatively nutrient-rich soils was initially successful. It is, however, not known whether these species can persist in the long term or whether a few dominant species will dominate the vegetation after several years. To answer this question it is of high importance to assess the ongoing floristic succession on the restoration sites for another period of five or more years.

Ecological significance of flooding

Our hypothesis that, owing to the input of diaspores via flooding, species-enrichment will be more successful in the functional flood-plain could not be confirmed (chapter 4). Species-richness per plot was even significantly lower in the functional flood-plain than in the fossil flood-plain. Thus, for our study area there seems to be generally little hope that the input of diaspores via flooding will enhance restoration perspectives. Comparable conclusions were drawn by Vécrin et al. (2002) in a flood-meadow restoration project in NE France. For species-rich wet heathlands van Duren (1998) also found that restoration of the former hydrological conditions did not result in species-enrichment and that an input of species via dispersal by flooding or from the seedbank could not be expected. In our case the lack of substantial seed sources of target-species along the largely confined Upper Rhine and in close proximity to the restoration sites must be seen as the main factor for the subordinate role of floods as dispersal vector. Furthermore the remnants of upstream species-rich flood-meadows are mostly restricted to dyked fossil compartments (Thomas 1990). The considerable distance of most of our study plots from the main channel and their spatial separation from water

courses by alluvial forests may also hamper the arrival of propagules in the course of flooding events (Bakker et al. 2002). For the same reason most of the restoration sites are hardly reached by substantial loads of nutrient containing mineral and organic sediments. This must be seen as a positive effect since the goal of lowering the soil nutrient status during restoration is not negatively affected by flooding.

Moreover, our seedbank study of irregularly flooded arable fields (chapter 5) suggested that even short distance dispersal by flooding seemed to be ineffective. The sites where seedbank samples were taken, were situated in the near vicinity but the similarity between the seedbanks showed insignificance, which means that there was no input of diaspores from adjacent fields via flooding or other dispersal modes. This result is in line with Bischoff (2002) who found for grasslands in the flood-plain of the Saale river that even in the proximity of remnant populations, flooding does not significantly enhance the effectiveness of short distance dispersal. In another seedbank study along the northern Upper Rhine, Hölzel & Otte (2001) found no evidence of long-distance dispersal by flooding. In the same study short-distance dispersal by inundation was found to be a more relevant process since many seeds of arable weeds occurred in the seedbank of study plots which have never been subject to agricultural use.

The divergence of findings suggests that the importance of flood dispersal, in particular short-distance dispersal, for the restoration of wet grasslands still needs further clarification. Generally, it appears to be advantageous to have species-rich flood-meadows or viable remnant populations of target species that may function as seed sources close to the restoration sites. According to this study, rare events of long-distance transport can not be entirely excluded but there it seems to be unlikely that flooding may enhance species-enrichment at the restoration sites in the near future.

The relative importance of the seedbank

The seedbank study (chapter 6) showed that only few perennial species typical of flood meadows (such as *Juncus inflexus*, *Juncus compressus, Agrostis stolonifera, Mentha aquatica*) were found in the seedbank of arable fields, including only *Pseudolysimachion longifolium* as endangered target-species of flood-meadows. This highlights the low potential of the studied seedbank for the restoration of species rich flood-meadows alone from the soil seedbank. Our results are supported by a study of Hölzel & Otte (2001) who investigated the seedbank of sites situated in three different hydrological compartments of the Holocene flood-plain along the Upper Rhine. Only certain flood-meadow species, which are

characterized by a ruderal strategy and typically exploit gaps in the established vegetation caused by flooding events, rely on persistent seedbanks (e.g. *Arabis nemorensis* or *Cerastium dubium*) (Hölzel & Otte 2004a). Even under favourable marginal conditions about 60 % of the target species are not able to built up a persistent seedbank (Hölzel & Otte 2004a; Fuhr-Boßdorf 2003).

As pointed out by other authors there is only a limited potential for restoration of semi-natural grassland in the soil seedbank because the majority of target species build up transient or short term persistent seedbanks (Graham & Hutchings 1988; Bakker et al. 1996; Thompson 1993). This applies to a wide range of grassland types, reaching from e.g. wet *Cirsio-Molinietum* fens (van Duren 1998) or salt marsh areas (Bakker 1989) up to dry mediterranean steppe communities (Römermann 2005). Particularly after several years or decades of intensive arable use with fertilization or drainage it seems unlikely that diaspores have persisted in the soil seedbank (Pfadenhauer & Maas 1987; Mc Donald et al. 1996; Bekker et al. 1997; Waldhardt et al. 2001).

However, for the long-term conservation of the studied ephemeral wetland vegetation in arable fields, which contains a number of endangered species (e.g. *Samolus valerandi*, *Centaurium pulchellum*, *Coronopus squamatus*) (Korneck et al. 1996), the large persistent soil seedbank proved to be of outstanding importance. In contrast to many flood-meadow species, a large number of ephemeral mudflat species are well known to build up large persistent soil seedbanks and to be able to germinate directly after drawdown (van der Valk & Davis 1978; Casanova & Brock 2000; Jutila 2001). Therefore measurements for the preservation of these species have to focus on the maintenance and renewal of the seedbank. In contrast to mudflat plants in primary habitats, which are able to reproduce also in years with only slight drawdown at exposed edges of oxbows and river banks, in secondary habitats successful reproduction and thus replenishment of the seedbank is restricted to years with extremely long lasting floods of the Rhine. At these sites improved drainage and landfill as well as early re-ploughing of the fields threatens the occurrence of mudflat vegetation. Thus for the successful conservation of ephemeral wetland vegetation the maintenance of low-lying arable fields in the flood-plain which are subject to moderate agricultural management is of high importance. Since mudflat communities are also in constant decline (Täuber & Petersen 2000; Poschlod et al. 1996) this should be considered in grassland restoration projects.

Recruitment in grassland swards

In our experiment low germination and establishment rates (< 7%) in the species-poor meadows demonstrated a lack of suitable microsites in the grassland sward (chapter 6). In contrast, similar experiments in adjacent ex-arable fields revealed a much higher recruitment success (Donath et al., submitted). The lack of competition from neighbouring plants, mainly grasses, and a more open sward may be the reason for these differences (Tilman 1993; Křenová & Lepš 1996; Kotorová & Lepš 1999). Surprisingly the applied management regimes showed only a weak effect on seedling recruitment. In many studies, cutting was found to facilitate seedling recruitment by the creation of open gaps and weakening of competitors (Bakker et al. 1980; Hutchings & Booth 1996; Lawson et al. 2004). In our experiment an effect of competitive release by mowing twice was only found in the first study year, when biomass production was much higher than in the second year.

Conversely, in alluvial grasslands along the northern Upper Rhine other environmental factors, like flooding and drought seem to control seedling germination and establishment to a larger extent. Due to the extremely dry and warm summer 2003, which caused desiccation and rapid hardening of the soils, seedling survivorship was extremely low. Similarly, in dry calcareous grasslands, summer drought was found to be the main cause for high seedling mortality (Silvertown & Dickie 1981; Ryser 1993). Generally, a constant moisture supply has a very positive impact on seedling recruitment (Oomes & Elberse 1976; De Jong & Klinkhammer 1988) while in the studied flood-meadows such conditions mostly prevail after irregularly occurring periods of spring and early summer flooding. Therefore, temporal variation in annual flooding along with the stochasticity of climate, result in a high variability of soil moisture conditions. This is obviously the most crucial constraint of seedling recruitment in the studied alluvial grasslands. For the restoration of wet fen meadows Patzelt et al. (2001) also found that a stable water level, close to the surface, is a prerequisite for the successful establishment of fen species.

Our results suggested that the high spatio-temporal variability of site conditions in flood-plains induced occasionally occurring events of successful recruitment whereas in other cases establishment may be poor or even fail completely in many seasons. Thus a temporal replication of restoration measures such as sowing of seeds or diaspore transfer of plant material may enhance restoration success. Furthermore, to improve recruitment conditions particularly soil moisture conditions, temporary irrigation in the first year of establishment could probably also be helpful.

Generally, the study clearly showed that even if seeds from target-species were re-introduced by sowing the recruitment success was not guaranteed. This is particularly true for closed existing grassland swards, which requires heavy disturbances to ensure recruitment. In contrast early stages of arable field succession seem to be much more favourable for the successful establishment of target species (Pywell et al. 2002; Walker et al. 2004; Hölzel, accepted).

Management practices in alluvial grasslands

For the conservation of endangered semi-natural grassland species it is of major interest to evaluate the suitability of different management regimes. A useful methodically approach in this context, is the investigation of plant population stage structure of perennial plants in relation to management. We studied the population stage structure of the model species *Serratula tinctoria* in meadows with three different types of grassland management (chapter 7). The results showed that viable populations of *S. tinctoria* do occur in early as well as in late mown meadows while in the meadow pastures clonal propagation seemed to be of higher significance. Although other authors have reported a sensitivity of *S. tinctoria* to early mowing (Briemle & Ellenberg 1994), our findings in the Upper Rhine valley suggest a clear facilitation of the species by mowing in June at more nutrient-rich sites (alliance *Cnidion*). For several other target species of flood-meadows (e.g. *Silaum silaus, Inula salicina, Allium angulosum)* an early first cut also proved to be advantageous (Joyce 1998; Hölzel et al. 2002). All these species exhibit the ability for successful vegetative regeneration, flowering and seed production during the second growth in late summer and may benefit from competitive release after mowing. Even highly endangered *Viola*-species such as *Viola pumila* are characterized by a flexible seed production since they produce cleistogamous flowers (Hölzel 2003; Eckstein & Otte, in press). This suggests that only species lacking both the ability to produce seeds after a first cut in June and the ability to propagate clonally depend on a late first cut to reproduce successfully.

Early mowing also strongly improves the prospects for an integration of management and biomass in existing farming systems. As shown by Donath et al. (2004) due to relatively high yields and a good forage quality, hay from flood-meadows can be readily incorporated as basic fodder in feeding-systems of cattle and horses. In contrast, restrictive management guidelines are often associated with a late first cut and a subsequent loss in forage quality even if there is no need to do so. Thus, generally more flexible management schemes should be employed and evaluated.

In relatively unproductive sites like fen meadows or heathlands *S. tinctoria* may remain susceptible to early mowing. Therefore habitat- and species-specific requirements of endangered target species should always be taken into account before management recommendations are given. Moreover, early management often conflicts with zoological interests, in particular ground nesting birds and many invertebrates depend on late mowing and a tall vegetation structure in early summer. Here, the setting of clear conservation targets is of high importance for the implementation of appropriate management practices (Bakker & Berendse 1999).

8.2 Perspectives

Limited dispersal was found to be the major constraint in the restoration of species-rich alluvial grasslands. We concluded that supplementary measures such as sowing of seeds or diaspore transfer with plant material are necessary to overcome dispersal limitation. As shown by Hölzel & Harnisch (2002) and Hölzel & Otte (2003) plant material transfer proved to be a highly promising method for the restoration of flood-meadows on former arable fields along the northern Upper Rhine. This method also offers a high potential and numerous perspectives for restoration of semi-natural grasslands in general and even other habitat types.

Since it is not known whether restoration on formerly fertilized and relatively productive arable fields is successful and whether initially established populations can persist in the long run, long-term studies on population dynamics are necessary to elucidate the ongoing processes on the restoration sites. These studies should focus on the role of reproduction by seeds or clonal propagation and on the effects of competition from other plants. Population viability analysis (PVA) may be a useful tool to identify threats to population persistence and to assess the success of restoration measures (Menges 2000). PVA could be combined with fertilization experiments into an experimental demographic approach. How disturbances by management or flooding might affect these ‘new’ populations during succession is a further scientific question.

Additional work should also concentrate on the further spread and fate of target species at the restoration sites. It is important to know how fast initially established species are able to colonize the entire restoration site. With respect to alluvial meadows we should again focus on the importance of short-distance dispersal by flooding for restoration success which still remains unclear. Direct measurements by e.g. using seed traps, may give valuable information about the actual deposition of diaspores on a restoration site. Information about composition

and abundance of dispersed diaspores should be related to the established vegetation to assess the significance of dispersal by flooding.

Another practical question which arose from our results is how restoration success in existing grasslands can be improved. In the seed addition experiment microsite limitation in species-poor grassland was revealed as the main factor responsible for the low recruitment success. Competition from grasses and a high spatio-temporal variability of site conditions, including extreme events such as flooding and drought, could be the reasons for the failure of recruitment. Hence for a successful restoration of existing grasslands the sward has to be disturbed by milling or ploughing before seed addition to reduce competition from the surrounding grasses and to create favourable conditions for seedling recruitment. Further field research is required to study the effect and significance of different disturbance regimes on seedling recruitment in grassland swards.

Finally it is of crucial importance to evaluate management practices that optimize local survival of remaining populations. Even a successful restoration is dependent on remaining viable populations of target species since these populations may function as local seed source. Although the analysis of population stage structure of perennial plants only provided a short-term insight into demographic processes of *Serratula tinctoria,* the results of this study and several other studies (Bühler & Schmid 2001; Hegland et al. 2001) showed that it is a useful tool to evaluate different management regimes. Additionally, temporal replication of such studies might be helpful to assess the impact on environmental variation and extreme events.

9 Summary

Restoration attempts aiming at the recovery of species-rich alluvial grasslands along the northern Upper Rhine were evaluated with regard to the effects of flooding and management on plant dispersal and seedling recruitment. The overall aim of the studies was to assess the limiting abiotic and biotic constraints to the restoration of species-rich flood-plain communities.

As a starting point for further studies large-scaled restoration measures on former arable fields were evaluated by analysing floristic composition and soil nutrient status of old and newly established meadows in the functional and fossil flood-plain. Whereas the functional flood-plain is exposed to direct flooding which allows a free input of diaspores, the fossil flood-plain is protected from direct flooding by a dyke and only submerged by ascending groundwater. After 15-20 years of restoration management a low restoration success was found and target species largely failed to establish. This can not be explained by unsuitable edaphic site conditions since old and new meadows differed only slightly in environmental variables. Consequently, limited dispersal and recruitment could be identified as the main constraints for restoration. No evidence was found that species enrichment is enhanced via the input of diaspores by flooding in the functional flood-plain.

A study of the seedbanks of arable fields in the study area underpinned a minor importance of the soil seedbank for restoration of species-rich alluvial grasslands. However, for the persistence of ephemeral mudflat vegetation in irregularly flooded arable fields, which is another type of rare and endangered wetland vegetation, the seedbank proved to be of high significance. Most species found in these ephemeral communities build up large persistent seedbanks and are characterized by short life cycles as well as the ability to rapidly exploit periods of favourable conditions for germination and growth. Improved drainage, landfill and early re-ploughing of the fields threatens the occurrence of mudflat vegetation in irregularly submerged arable fields. Thus for the successful conservation of ephemeral wetland vegetation the maintenance of low-lying arable fields in the flood-plain which are subject to moderate agricultural management is of high importance.

Besides the availability of substantial seed sources, the lack of suitable microsites for seedling recruitment was identified as another limiting factor in restoration of semi-natural grasslands. In a seed addition experiment we studied the effects of different mowing regimes on seedling recruitment of six typical flood-meadow species in two alluvial grasslands with different flooding regimes. Generally, we found low germination rates suggesting a lack of suitable

microsites in the closed swards and a weak effect of the applied management regimes. Competitive release by mowing twice was only found in the first study year, when biomass production was much higher than in the second year. Moreover physical hazards such as flooding and drought seemed to control seedling germination and establishment to a large extent. Our findings suggest that the high spatio-temporal variability of site conditions in flood-plains result in irregularly occurring events of successful recruitment, which are essential for the persistence of many characteristic flood-meadow species.

The evaluation of management schemes is of high practical relevance for a successful conservation and maintenance of endangered semi-natural grassland species and communities. In this context the viability of target species populations may serve as a particularly useful indicator. We studied the stage structure of 24 populations of the threatened perennial *Serratula tinctoria* in alluvial meadows with respect to vegetation and management. Generally, we found only slight differences between the population stage structure of *S. tinctoria* in early and late mown meadows. Both management types had high densities of seedlings. In contrast, the meadow pastures had significantly lower densities of seedlings but relatively high densities of juveniles and vegetative adults, indicating a higher importance of clonal propagation under grazing pressure. The results showed that viable populations of *S. tinctoria* may occur in all of the studied management regimes. Although *S. tinctoria* was traditionally considered to be highly sensitive to early mowing, our results suggested a facilitation of the species by early mowing at more nutrient-rich sites.

The results of the present study documented that along the northern Upper Rhine mainly biotic constraints, i.e. the lack of seed sources in the vicinity of restoration sites and in the seedbank, hamper successful restoration of alluvial grasslands. In existing species-poor grassland swards microsite limitation is another seriously hampering factor. Finally we confirmed that the existing management regimes in the study area are appropriate for the maintenance of target species.

10 Zusammenfassung

In der vorliegenden Arbeit werden Renaturierungsmaßnahmen am nördlichen Oberrhein, die eine Wiederherstellung von artenreichen, auenspezifischen Grünlandphytocoenosen zum Ziel haben, evaluiert. Das übergeordnete Ziel der Arbeit ist es die Ursachen für den geringen Renaturierungserfolg und die limitierenden abiotischen und biotischen Faktoren herauszustellen. Die dabei zugrundeliegende Haupthypothese der Arbeit besagt, dass der geringe Erfolg der Renaturierungsmaßnahmen auf eine Ausbreitungslimitierung von Zielarten zurückzuführen ist. Die Bedeutung weiterer potentiell limitierender Faktoren, wie die hohe Nährstoffversorgung der Böden, die geringe Samenbankpersistenz von Zielarten in Böden sowie der Mangel an Regenerationsnischen sollen analysiert werden. Ein weiteres Ziel ist es die Rolle des Diasporeneintrages bei Überflutungen, mit dem hohe Renaturierungserwartungen verbunden sind, sowie die Effekte einer Nutzung auf die Samenproduktion und Etablierung von Zielarten zu untersuchen.

Seit Mitte der 80er Jahre wurden im Bereich der hessischen Rheinauen mit der Umwandlung von ackerbaulich genutzten Flächen in Grünland und der gleichzeitig erfolgenden Extensivierung der Flächen großflächig Renaturierungsmaßnahmen eingeleitet. Durch den Vergleich von den Renaturierungsflächen (Neuwiesen) mit artenreichen Altwiesen erfolgt eine Evaluierung der im Projektgebiet durchgeführten Maßnahmen. Ziel dieser Erfolgskontrolle ist es, wesentliche Erkenntnisse für das zukünftige Renaturierungsmanagement zu gewinnen. Hierzu wurden die Neuwiesen hinsichtlich biotischer (Artenzusammensetzung, Biomasseproduktion) und standörtlicher Merkmale (Nährstoffversorgung der Böden) mit leitbildnahen Altbeständen verglichen. Des weiteren wurden die jungen Renaturierungsflächen in der Rezent- und Altaue vergleichend analysiert um zu klären, ob der Diasporeneintrag bei Überflutungen einen entscheidenden Beitrag zur Wiederherstellung artenreicher Auengrünlandgesellschaften aus Äckern leisten kann. In der Rezentaue werden die Flächen bei Hochwasserereignissen direkt vom sedimentreichen Rheinwasser überflutet. Ein Eintrag von Diasporen und Sedimenten kann also stattfinden. In der Altaue dagegen werden die Flächen nur geringmächtig von klarem Druckwasser überstaut und ein Eintrag von Diasporen und Sedimenten ist daher ausgeschlossen.
Wertbestimmende Arten der Stromtalwiesen konnten sich in den vor ca. 20 Jahren neugeschaffenen Wiesenflächen nicht oder nur in sehr geringem Umfang etablieren. In den Neuwiesen dominieren nach wie vor die angesäten Gräser sowie einige Acker- und

Ruderalarten. Auch weit verbreitete, wenig anspruchsvolle Grünlandarten wie *Sanguisorba officinalis*, *Rumex acetosa* oder *Centaurea jacea* konnten sich auf den Renaturierungsflächen nicht etablieren. Dies trifft sowohl für die Renaturierungsflächen der Altaue als auch der Rezentaue zu. Im Gegensatz zu anderen Studien, welche die Bedeutung der Aushagerung nährstoffreicher Standorte für eine erfolgreiche Wiederansiedlung von Zielarten hervorheben, konnten hier nur geringe Unterschiede hinsichtlich der Biomasseproduktion und Nährstoffversorgung zwischen Alt- und Neuwiesen gefunden werden. Es konnte kein messbar höherer Renaturierungserfolg durch den Eintrag von Diasporen bei Hochwasserständen des Rheins in der Rezentaue nachgewiesen werden. Die gemachten Befunde erhärten die Hypothese, dass der mangelnde Renaturierungserfolg vornehmlich auf eine Ausbreitungslimitierung von Zielarten zurückzuführen ist. Aufgrund des starken Rückgangs von potentiellen Spenderbeständen entlang der großen zentraleuropäischen Flüsse kann selbst in den überflutungsgeprägten Stromtalwiesen die Ausbreitungslimitierung nicht durch die Wiederherstellung des natürlichen Überflutungsregimes überwunden werden.

Untersuchungen zur Bodendiasporenbank auf ackerbaulich genutzten Flächen haben gezeigt, dass nur sehr wenige Zielarten in der Samenbank vorhanden sind. Einige Zielarten können zwar eine persistente Diasporenbank bilden, diese wird aber besonders unter Ackernutzung schnell abgebaut. Damit erweist sich auch das von Samenbanken ausgehende Renaturierungspotential zur Wiederherstellung artenreicher Auenwiesen am nördlichen Oberrhein als äußerst gering. Für die Erhaltung ephemerer Schlammflur-Gesellschaften dagegen, die auf den untersuchten Überflutungsäckern auftreten und einen weiteren gefährdeten Vegetationstyp darstellen, ist die Samenbank von hoher Bedeutung. Neben Primärhabitaten von Schlammflur-Gesellschaften, wie z. B. Flussufer und Teichböden, sind Schlammfluren am nördlichen Oberrhein auch in tiefliegenden, periodisch überschwemmten Ackerflächen zu finden. Die Ergebnisse aus Vegetations- und Samenbankanalysen von Äckern, auf denen sich im Jahr 2001 nach einer Überflutung im Frühjahr Schlammflur-Gesellschaften etabliert hatten zeigen, dass neben charakteristischen Arten der Schlammfluren auch Ackerarten die Samenbank dominieren. Viele Arten der Schlammfluren bilden eine persistente Samenbank aus und sind durch kurze Lebenszyklen sowie hohe Reproduktionsraten charakterisiert. Damit können diese Arten kurze Perioden günstiger Feuchtebedingungen für Keimung und Wachstum ausnutzen. Die gefundenen Samendichten waren sehr hoch, wobei die häufigsten Arten *Juncus bufonius*, *Ranunculus sceleratus* und *Veronica catenata* waren. Für *Juncus bufonius* konnte beispielsweise eine extrem hohe

Samendichte von 707072 Samen/m² nachgewiesen werden. Die Untersuchungen verdeutlichen die hohe Bedeutung zeitweise überfluteter Äcker als Sekundärhabitat für ephemere Schlammflurgesellschaften. Durch Entwässerungsmaßnahmen, irreversible Standortzerstörungen (z. B. Schuttablagerung, Auffüllung von Senken), Nutzungsintensivierung (z. B. das sehr frühe Pflügen der Felder) aber auch durch die Aufgabe der landwirtschaftlichen Nutzung sind diese Standorte heute stark gefährdet. Für den langfristigen Schutz der Schlammflur-Gesellschaften ist daher die Erhaltung tiefliegender, periodisch überschwemmter Äcker die landwirtschaftlich extensiv genutzt werden äußerst bedeutsam.

In einer weiteren Teilstudie wurde der Frage nachgegangen, in welchem Maße die Wiederansiedlung von seltenen Arten durch fehlende Regenerationsnischen im bestehenden Grünland limitiert ist. Dazu wurde die Keimung und Etablierung von sechs verschiedenen Stromtalarten in artenarmen Grünlandbeständen unter dem Einfluss drei verschiedener Managementregime (Mahd im Mai und August, Mahd im Juni, Mahd im September) untersucht. Es wurde je ein faktorielles Aussaatexperiment auf einer Grünlandfläche in der Rezent- und Altaue angelegt, wobei die aufkommenden Keimlinge über einen Zeitraum von zwei Jahren beobachtet wurden.

Die angewendeten Mahdvarianten hatten nur geringe Auswirkungen auf die Keimungs- und Etablierungsraten der Stromtalwiesenarten. Es ergaben sich nur sehr geringe Keimungsraten, die besonders niedrig im Fall der kleinsamigen Art *Inula salicina* waren. Die Ergebnisse deuten darauf hin, dass die Zahl geeigneter Regenerationsnischen begrenzt ist und ein Grund für die geringe Etablierungsrate ist. Insbesondere der starke Konkurrenzdruck der Gräser in der weitgehend geschlossenen Grasnarbe lässt nur in geringem Umfang eine erfolgreiche Etablierung der Keimlinge zu. Signifikante Effekte der verschiedenen Mahdregime wurden nur im ersten Untersuchungsjahr beobachtet, in dem die Biomasseproduktion deutlich höher als im zweiten Jahr war. Während des ersten Zeitraums führte eine zweimalige Mahd (Mai, August) zu einer höheren Keimlingsdichte.

Im Gegensatz zu den geringen Effekten der durchgeführten Behandlungsvarianten scheinen natürliche nicht kontrollierbare Ereignisse wie Trockenheit und Überflutung von weitaus größerer Bedeutung für die Keimung und Etablierung zu sein. So hat die ausgeprägte Sommertrockenheit im Jahr 2003 bei den meisten Arten zu einem deutlichen Rückgang der Keimlinge geführt. Die Ergebnisse deuten darauf hin, dass die hohe räumlich-zeitliche Variabilität der Umweltbedingungen einen sehr hohen Einfluss auf Keimung und Etablierung haben und somit die Vegetationszusammensetzung sehr stark beeinflussen.

Zur Klärung der Frage, ob die Nutzung ein weiterer limitierender Faktor für den Renaturierungserfolg und für die dauerhafte Erhaltung der Stromtalwiesen darstellt, ist es von großem praktischem Interesse die Wirkung verschiedener Nutzungstypen auf Zielarten zu bewerten. Hierfür ist eine Analyse des demographischen Zustands ausgewählter Zielarten und damit die Untersuchung der Überlebensfähigkeit von Populationen ein wichtiger und nützlicher Indikator. In Stromtalwiesen entlang des nördlichen Oberrhein wurde die Populationsstruktur von 24 Populationen der gefährdeten Art *Serratula tinctoria* in Beziehung zur bestehenden Vegetation und verschiedenen Managementtypen untersucht. Die Grünlandbestände kennzeichneten sich durch folgende Nutzungstypen: a) Spätmahd im September, b) frühe Mahd im Juni, c) Mahd im Juni und Nachbeweidung durch Schafe im Herbst.

Es ergaben sich keine signifikanten Unterschiede zwischen der Populationsstruktur von früh und spät gemähten Wiesen. Beide Nutzungstypen waren durch eine hohe Anzahl von Keimlingen charakterisiert. Im Gegensatz dazu zeichneten sich die im Juni gemähten und anschließend beweideten Wiesen durch einen signifikant niedrigeren Prozentanteil an Keimlingen, aber einen relativ hohen Anteil an Juvenilen und vegetativ Adulten aus. Dies verdeutlicht, dass unter Beweidungsdruck vermehrt klonales Wachstum stattfindet. Die Ergebnisse geben klare Hinweise, dass sich überlebensfähige Populationen sowohl in spätgemähten als auch in frühgemähten Wiesen entwickeln können. Tendenziell ermöglichen alle Managementregime die Produktion von Samen und bieten günstige Etablierungsbedingungen. Im Fall der im Frühsommer gemähten Wiesen stehen diese Ergebnisse im Widerspruch zu den traditionellen pflanzensoziologischen Angaben, welche *S. tinctoria* als „nur Herbstmahd vertragend“ bezeichnen. In produktiven Auenwiesen am nördlichen Oberrhein (Verband *Cnidion*) scheint sich jedoch eine Mahd im Juni deutlich positiv auf die Populationsstruktur auszuwirken. Gleichermaßen verbessert eine frühe Mahd die Möglichkeiten, das Management und die anfallende Biomasse in bestehende landwirtschaftliche Strukturen einzubinden.

Die Ergebnisse der Arbeit zeigen deutlich, dass am nördlichen Oberrhein vorwiegend biotische Faktoren, wie z. B. das Fehlen von Diasporen von Zielarten in der Umgebung der Renaturierungsflächen sowie in der Bodendiasporenbank für den geringen Renaturierungserfolg verantwortlich sind. Aus diesem Grunde ist eine erfolgreiche Renaturierung von artenreichem Auengrünland zeitnah nur durch zusätzliche Maßnahmen wie eine Einsaat von Zielarten oder durch die Ausbringung von diasporenhaltigem Mahdgut zu

erreichen. Neben dieser Samenlimitierung wird die Artenanreicherung in bestehenden artenarmen Grünlandflächen zusätzlich durch das Fehlen von geeigneten Regenerationsnischen limitiert. Für eine erfolgreiche Artenanreicherung im bestehenden Grünland sind daher Maßnahmen, die eine nachhaltige Störung der Grasnarbe bewirken für eine erfolgreiche Etablierung von Stromtalwiesenarten förderlich.

Ferner konnte mit dieser Arbeit bestätigt werden, dass die bestehenden Nutzungstypen im Untersuchungsgebiet eine erfolgreiche Reproduktion und Etablierung der Zielarten zulassen und geeignet für die Erhaltung der Stromtalwiesen sind.

11 References

Abernethy, V.J. & Willby, N.J. 1999. Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. *Plant Ecol.* 140: 177-190.

Andersson, E., Nilsson, C. & Johansson, M.E. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *J. Biogeogr*. 27: 1095-1106.

Anon. 1993. *Faustzahlen für Landwirtschaft und Gartenbau.* Landwirtschaftsverlag GmbH, Münster-Hiltrup, DE.

Anon. 1998. *STATISTICA for Windows*. 5.1, Statsoft Inc., Tulsa, OK, US.

Anon. 1999. *SAS for Windows*. 8.2, SAS Institute Inc., Cary, NC, US.

Anon. 2002. *STATISTICA for Windows*. 6.0, Statsoft Inc., Tulsa, OK, US.

Bakker, J.P., Dekker, M. & De Vries, Y. 1980. The effect of different management practices on a grassland community and the resulting fate on seedlings. *Acta Bot. Neerl.* 29: 469-482.

Bakker, J.P. 1989. *Nature Management by Grazing and Cutting. On the ecological significance of grazing and cutting regimes applied to restore former species-rich grassland communities in the Netherlands.* Kluwer, Dordrecht, NL.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. 1996. Seed banks and seed dispersal: Important topics in restoration ecology. *Acta Bot. Neerl.* 45: 461-490.

Bakker, J.P. & Berendse, F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* 14: 63-68.

Bakker, J.P., Esselink, P., Dijkema, K.S., van Duin, W.E. & De Jong, D.J. 2002. Restoration of salt marshes in the Netherlands. *Hydrobiologia* 478 (1-3): 29-51.

Baskin, C.C. & Baskin, J.M. 2001. *Seeds - Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, US.

Bastrenta, B. 1991. Effect of sheep grazing on the demography of *Anthyllis vulneraria* in southern France. *J. Ecol.* 79: 275-284.

Bekker, R.M., Verweij, G.L., Smith, R.E.N., Reine, R., Bakker, J.P., Schneider S. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? *J. Appl. Ecol.* 34: 1293-1310.

Bekker, R.M., Verweij, G.L., Bakker, J.P. & Fresco, L.F.M. 2000. Soil seed bank dynamics in hayfield succession. *J. Ecol.* 88: 594-607.

Berendse, F., Oomes, M.J.M., Altena, H.J. & Elberse, W.T. 1992. Experiments on the restoration of species-rich meadows in The Netherlands. *Biol. Conserv.* 62: 59-65.

Bernhardt, K.G. 1993. Populationsökologische Untersuchungen an *Juncus bufonius* an sekundären Abgrabungsstandorten. *Zeitschr. Ökol. Natursch.* 2: 157-162.

Bischoff, A. 2002. Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biol. Conserv.* 104: 25-33.

Blom, C. & Voesenek, L. 1996. Flooding: The survival strategies of plants. *Trends Ecol. Evol.* 11: 290-295.

Böger, K. 1991. *Grünlandvegetation im Hessischen Ried - pflanzensoziologische Verhältnisse und Naturschutzkonzeption. Botanik und Naturschutz in Hessen*, Beiheft 3, Botanische Vereinigung für Naturschutz in Hessen e.V. (BVNH), Frankfurt a. M., DE.

Bonis, A., Lepart, J. & Grillas, P. 1995. Seedbank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. *Oikos* 74: 81-92.

Bonn, S. & Poschlod, P. 1998. *Ausbreitungsbiologie der Pflanzen Mitteleuropas.* Quelle & Meyer, Wiesbaden, DE.

Bornette, G., & Amoros, C. 1996. Disturbance regimes and vegetation dynamics: Role of floods in riverine wetlands. *J. Veg. Sci.* 7: 615-622.

Bosshard, A. 2000. Blumenreiche Heuwiesen aus Ackerland und Intensiv-Wiesen - Eine Anleitung zur Renaturierung in der landwirtschaftlichen Praxis. *Natursch. Landschaftspl.* 32: 161-171.

Briemle, G. & Ellenberg, H. 1994. Zur Mahdverträglichkeit von Grünlandpflanzen. Möglichkeiten der praktischen Anwendung von Zeigerwerten. *Nat. Landsch.* 69: 139-147.

Briemle, G., Nitsche S. & Nitsche G. 2002. Nutzungswertzahlen für Gefäßpflanzen des Grünlandes. *Schriftenr. Vegetationsk*. 38: 203-225.

Bühler, C. & Schmid, B. 2001. The influence of management regime and altitude on the population structure of *Succisa pratensis*: implications for vegetation monitoring. *J. Appl. Ecol.* 38: 689-698.

Bullock, J.M., Clear Hill, B., Dale, M.P. & Silvertown, J. 1994. An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *J. Appl. Ecol.* 31: 493-507.

Bullock, J.M., Hill, B.C., Silvertown, J. & Sutton, M. 1995. Gap colonization as a source of grassland community change - effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* 72: 273-282.

Burkart, M. 1998. *Die Grünlandvegetation der unteren Havelaue in synökologischer und syntaxonomischer Sicht.* Martina Galunder Verlag, Wiehl, DE.

Burkart, M. 2001. River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Global Ecol. Biogeogr.* 10: 448-468.

Cain, M.L., Milligan, B.G. & Strand, A.E. 2000. Long-distance seed dispersal in plant populations. *Am. J. Bot.* 87: 1217-1227.

Casanova, M.T. & Brock, M.A. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecol.* 147: 237-250.

Cavers, P.B. & Benoit, D.L. 1989. Seedbanks in Arable Land, In: Leck M.A., Parker V.T. & Simpson R.L. (eds.) *Ecology of Soil Seedbanks*, pp. 309-328. Academic Press, San Diego, US.

Chippendale, H.J. & Milton, W.E.J. 1934. On the viable seeds present in the soil beneath pastures. *J. Ecol.* 22: 508-531.

Colling, G., Matthies, D. & Reckinger, C. 2002. Population structure and establishment of the threatened long-lived perennial *Scorzonera humilis* in relation to environment. *J. Appl. Ecol.* 39: 310-320.

Coulson, S.J., Bullock, J.M., Stevenson, M.J. & Pywell, R.F. 2001. Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *J. Appl. Ecol.* 38: 204-216.

Critchley, C.N.R., Chambers, B.J., Fowbert, J.A., Sanderson, R.A., Bhogal, A. & Rose, S.C. 2002. Association between lowland grassland plant communities and soil properties. *Biol. Conserv.* 105: 199-215.

De Jong, T. & Klinkhamer, P.G.L. 1988. Seedling establishment of the biennials *Cirsum vulgare* and *Cynoglossum officinale* in a sand-dune area: The importance of water for differential survival and growth. *J. Ecol.* 76: 393-402.

Dister, E. 1980. Geobotanische Untersuchungen in der hessischen Rheinaue als Grundlage für die Naturschutzarbeit. Doctoral thesis, Göttingen, DE.

Dister; E., Schneider, E., Schneider, E., Fritz, H.-G., Winkel, S., Flößer, E. 1992. Wissenschaftliche Erfahrungen aus Renaturierungsprojekten. Großflächige Renaturierung des „Kühkopfes“ in der hessischen Rheinaue - Ablauf, Ergebnisse und Folgerungen der Sukzessionsforschung. *Beitr. Akad. Natur- und Umweltschutz B.-W.* 13 b: 20-36.

Donath, T.W., Hölzel, N. & Otte, A. 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Appl. Veg. Sci.* 6.1: 13-22.

Donath, T.W., Hölzel, N., Bissels, S. & Otte, A. 2004. Prospects for incorporating biomass from un-intensively managed flood-plain meadows in farming systems. *Agr. Ecosyst. Environ.* 104: 439-451.

Donath, T.W., Hölzel, N. & Otte, A. submitted. The influence of competition by sown grass, disturbance and litter on germination, early survivorship and final establishment in flood-meadow restoration.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.

During, H.J. & Van Tooren, B.F. 1990. Bryophyte interactions with other plants. *Bot. J. Linn. Soc.* 104: 79-98.

Eckstein, R.L., Danihelka, J., Hölzel, N. & Otte, A. 2004. The effects of management and environmental variation on population stage structure in three river-corridor violets. *Acta Oecol*. 25: 83-91.

Eckstein, R.L. & Otte, A. in press. The effects of cleistogamy and pollen source on seed production and offspring performance in three endangered violets. *Basic Appl. Ecol.*

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot.* 18: 1-248.

Eriksson, O. & Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91: 360-364.

Eriksson, O. 1997. Clonal life histories and the evolution of seed recruitment. In: De Kroon H. & van Groenendael J. (eds.) *The ecology and evolution of clonal plants*, pp. 1-29. Backhuys, Leiden, NL.

Fenner, M. 1978. A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. *J. Ecol.* 66: 953-963.

Fischer, S.F., Poschlod, P., Beinlich B. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *J. Appl. Ecol.* 33: 1206-1222.

Foster, B.L. 1999. Establishment, competition and the distribution of native grasses among Michigan old-fields. *J. Ecol.* 87: 476-489.

Fowler, N.L. 1988. What is a safe site?: Neighbor, litter, germination date, and patch effects. *Ecology* 69: 947-961.

Fuhr-Boßdorf, K. 2003: Die Bedeutung der Diasporenbank aktuell und ehemals landwirtschaftlich genutzter Standorte für Vegetationsentwicklungen im Lahn-Dill-Bergland (Hessen). PhD-Thesis, Univ. Giessen.

Gerritsen, J. & Greening, H.S. 1989. Marsh seedbanks of the Okefenokee Swamp: Effects of hydrologic regime and nutrients. *Ecology* 70: 750-763.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* 68: 1211-1223.

Goodson, J.M., Gurnell, A.M., Angold, P.G. & Morrissey, I.P. 2001. Riparian seedbanks: structure, process and implications for riparian management. *Prog. Phys. Geog.* 25: 301-325.

Goodson, J.M., Gurnell, A.M., Angold, P.G. & Morrissey, I.P. 2002. Riparian seedbanks along the lower River Dove, UK: their structure and ecological implications. *Geomorphology* 47: 45-60.

Gough, M.W. & Marrs, R.H. 1990. A comparison of soil fertility between semi-natural and agricultural plant communities: implications for the creation of species-rich grassland on abandoned agricultural land. *Biol. Conserv.* 51: 83-96.

Graham, D.J. & Hutchings, M.J. 1988. A field investigation of germination from the seed bank of a chalk grassland ley on former arable land. *J. Appl. Ecol.* 25: 253 - 263.

Grillas, P., Garcia-Murillo, P., Geertz-Hansen, O., Marba, N., Montes, C., Duarte, C.M., Tan Ham, L. & Grossmann, A. 1993. Submerged macrophyte seedbank in a Mediterranean temporary marsh: abundance and relationship with established vegetation. *Oecologia* 94: 1-6.

Grime, J.P. & Hodgson, J.G., Hunt, R. 1988. *Comparative Plant Ecology: A Functional Approach to Common British Species.* Unwin Hyman, London, UK.

Grime, J.P. 2002. *Plant strategies, vegetation processes, and ecosystem properties.* Wiley, Chichester, UK.

Gross, K.L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J. Ecol.* 72: 369-387.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev. Cambr. Philos. Soc.* 52: 107-145.

Güsewell, S., Zorzi, A. & Gigon, A. 2000. Mowing in early summer as a remedy to eutrophication in Swiss fen meadows: are really more nutrients removed? *Bull. Geobot. Inst. Eidg. Tech. Hochsch. Rübel Zür.* 66: 11-24.

Harper, J.L. 1977. *Population biology of plants.* Academic Press, London, UK.

Hegi, G. 1987. *Illustrierte Flora von Mitteleuropa: Pteridophyta, Spermatophyta*, *Compositae II: Matricaria - Hieracium VI*. Parey, Berlin, Hamburg, DE.

Hegland, S.J., Van Leeuwen, M. & Oostermeijer, J.G.B. 2001. Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *J. Appl. Ecol.* 38: 1277-1289.

Hoffmann, G. 1991. *Die Untersuchung von Böden – Methodenbuch 1.* VDLUFA-Verlag, Darmstadt, DE.

Hölzel, N. 1999. Flora und Vegetation der Auewiesen im NSG "Lampertheimer Altrhein" - eine aktuelle Zustandsanalyse mit Hinweisen zur zukünftigen Pflege und Entwicklung. *Jahrb. Nat. schutz Hessen* 4: 24-42.

Hölzel, N. & Otte, A. 2001. The impact of flooding regime on the soil seed bank of flood-meadows. *J. Veg. Sci.* 12: 209-218.

Hölzel, N. & Harnisch, M. 2002. Renaturierung von Stromtalwiesen. *Garten u. Landschaft* 12: 36-38.

Hölzel, N., Donath, T.W., Bissels, S. & Otte, A. 2002. Auengrünlandrenaturierung am hessischen Oberrhein - Defizite und Erfolge nach 15 Jahren Laufzeit. *Schriftenr. Vegetationsk.* 36: 131-136.

Hölzel, N. 2003. Re-assessing the ecology of the rare flood-meadow violets (*Viola elatior, V. pumila and V. persicifolia*) with large phytosociological data sets. *Folia Geobot.* 38: 281-298.

Hölzel, N. & Otte, A. 2003. Restoration of a species-rich flood-meadow by topsoil removal and diaspore transfer with plant material. *Appl. Veg. Sci.* 6: 131-140.

Hölzel, N. & Otte, A. 2004a. Ecological significance of germination characteristics in flood-meadow species. *Flora* 199: 12-24.

Hölzel, N. & Otte, A. 2004b. Assessing soil seed bank persistence in flood-meadows: The search for reliable traits. *J. Veg. Sci.* 15: 93-100.

Hölzel, N. accepted. Ecology of seedling recruitment in flood-meadow species - the effect of gaps, litter and vegetation matrix. *Appl. Veg. Sci.*

Hultén, E. & Fries, M. 1986. *Atlas of North European vascular plants north of the tropic of cancer.* Koeltz, Königstein, DE.

Hutchings, M. J. & Booth, K.D. 1996. Studies of the feasibility of re-creating chalk grassland vegetation on ex-arable land. *J. Appl. Ecol.* 33: 1182-1190.

Isselstein, J., Tallowin, J.R.B. & Smith, R.E.N. 2002. Factors affecting seed germination and seedling establishment of fen-meadow species. *Restor. Ecol.* 10: 173-184.

Jakobsson, A. & Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.

Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.P., Bekker, R.M., Fillat, F. & Oomes, M.J.M. 1998. Relationship between soil chemical factors and grassland diversity. *Plant Soil* 202: 69-78.

Jensen, H.A. 1969. Content of buried seeds in arable soil in Denmark and its relation to the weed population. *Dan. Bot. Ark.* 27: 1-56.

Jensen, K. 1998. Species composition of soil seed bank and seed rain of abandoned wet meadows and their relation to aboveground vegetation. *Flora* 193: 345-359.

Jensen, K. & Meyer, C. 2001. Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. *Plant Ecol.* 155: 169-181.

Johansson, M.E., Nilsson, C. & Nilsson, E. 1996. Do rivers function as corridors for plant dispersal? *J. Veg. Sci.* 7: 593-598.

Jones, A. T. & Hayes, M. J. 1999. Increasing floristic diversity in grassland: the effects of management regime and provenance on species introduction. *Biol. Conserv.* 87: 381-390.

Jongman, R.H.G., Ter Braak C.J.F. & Van Tongeren O.F.R. 1995. *Data analysis in community and landscape ecology.* Cambridge University Press, Cambridge, UK.

Joyce, C.B. 1998. Plant community dynamics of managed and unmanaged floodplain grasslands: an ordination analysis. In: Joyce, C.B., Wade, P.M. (ed.) *European wet grasslands: biodiversity, management and restoration*, pp. 173-191. Wiley, Chichester, UK.

Joyce, C.B., Wade; P.M. 1998. *European wet grasslands: biodiversity, management and restoration*. Wiley, Chichester, UK.

Jutila, H.M. 2001. Effect of flooding and drawdown disturbance on germination from a seashore meadow seedbank. *J. Veg. Sci* 12: 729-738.

Jutila, H.M. & Grace, J.B. 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *J. Ecol.* 90: 291-302.

Jutila, H.M. 2003. Germination in Baltic coastal wetland meadows: similarities and differences between vegetation and seed bank. *Plant Ecol*. 166: 275-293.

Kapfer, A. 1988. Versuche zur Renaturierung gedüngten Feuchtgrünlandes - Aushagerung und Vegetationsentwicklung. *Diss. Bot.* 120: 1-144.

Kellogg, C.H., Bridgham, S.D. & Leicht, S.A. 2003. Effects of water level, shade and time on germination and growth of freshwater marsh plants along a simulated successional gradient. *J. Ecol.* 91: 274-282.

Klimeš, L., Klimešová, J., Hendriks, R. & van Groenendael, J. 1997. Clonal plant architectures: a comparative analysis of form and function. In: De Kroon H. & van Groenendael J. (eds.) *The ecology and evolution of clonal plants*, pp. 1-29. Backhuys, Leiden, NL.

Knapp, R. 1954. Über Pflanzengesellschaften der Wiesen in Trockengebieten Deutschlands. *Angew. Pflanzensoz.* (*Aichinger Festschr.*) 2: 1145-1186.

Korneck, D., Vollmer, J. & Schnittler M. 1996. Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Deutschlands. *Schriftenr. Vegetationsk.* 28: 21-187.

Kotorová, I. & Lepš, J. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *J. Veg. Sci.* 10: 175-186.

Krenová, Z. & Lepš, J. 1996. Regeneration of a *Gentiana pneumonanthe* population in an oligothrophic wet meadow. *J. Veg. Sci.* 7: 107-112.

Kuntze, H., Roeschmann, G. & Schwerdtfeger, G. 1994. *Bodenkunde.* 5. ed. Ulmer, Stuttgart, DE.

Kupferschmid, A.D., Stampfli, A. & Newbery, D.M. 2000. Dispersal and microsite limitation in an abandoned calcareous grassland of the southern prealps. *Folia Geobot.* 35: 125-141.

Lambrecht, K. 1983. Landwirtschaftliche Standortverhältnisse und Entwicklung des Bewässerungslandbaus unter dem Einfluß eines veränderten Wasserhaushaltes im Hessischen Ried. Doctoral thesis, Gießen, DE.

Lawson, C.S., Ford, M.S., Mitchley, J. 2004. The influence of seed addition and cutting regime on the success of grassland restoration on former arable land. *Appl. Veg. Sci*. 7: 259-266.

Leck, M.A. & Graveline, K.J. 1979. The seedbank of a freshwater tidal marsh. *Am. J. Bot.* 66: 1006-1015.

Leck, M.A. & Simpson, R.L. 1987. Seedbank of a freshwater tidal wetland: Turnover and relationship to vegetation change. *Am. J. Bot.* 74: 360-370.

Leck, M.A. 1989. Wetland seedbanks, In: Leck M.A., Parker V.T. & Simpson R.L. (eds.) *Ecology of soil seedbanks*, pp. 283-305. Academic Press, San Diego, US.

Leck, M.A. & Simpson, R.L. 1995. Ten-year seedbank and vegetation dynamics of a tidal freshwater marsh. *Am. J. Bot.* 82: 1547-1557.

Legendre, P. & Legendre, L. 1998. *Numerical Ecology*, *Developments in Environmental Modelling 20*. 2nd ed. Elsevier, Amsterdam, NL.

Leishman, M.R., Wright, I.J. & Moles, A.T. 2000. The evolutionary ecology of seed size. In: M. Fenner (ed.), *Seeds - the ecology of regeneration in plant communities,* pp. 31-57. CAB International, Wallingford, Oxon, UK.

Lennartsson, T. & Oostermeijer, J.G.B. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *J. Ecol.* 89: 451-463.

Lepš, J. 1999. Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow copy. *J. Veg. Sci.* 10: 219-230.

Leyer, I. 2002. Auengrünland der Mittelelbe-Niederung: Vegetationskundliche und -ökologische Untersuchungen in der rezenten Aue, der Altaue und am Auenrand der Elbe. *Diss. Bot.* 363: 1-193.

Marrs, R.H. 1993. Soil fertility and nature conservation in Europe - theoretical considerations and practical management solutions. *Adv. Ecol. Res.* 24: 241-300.

McCune, B. & Mefford, M.J. 1999. *Handbook - PC-ORD Multivariate Analysis of Ecological Data.* MjM Software, Gleneden Beach, OR, US.

McCune, B. & Grace, J.B. 2002. *Analysis of Ecological Communities.* MjM Software, Gleneden Beach, OR, US.

McDonald, A.W., Bakker, J.P. & Vegelin, K. 1996. Seed bank classification and its importance for the restoration of species-rich flood-meadows. *J. Veg. Sci* 7: 157-164.

McGraw, J.B. 1987. Seedbank properties of an Appalachian Sphagnum bog and a model of the depth distribution of viable seeds. *Can. J. Botany* 65: 2028-2035.

Menges, E. S. 2000. Population viability analyses in plants: challenges and opportunities. *Trends Ecol. Evol.* 15: 51-56.

Meyer, A. H. & Schmid, B. 1999. Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. *J. Ecol.* 87: 28-41.

Moles, A. T. & Westoby, M. 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99: 241-248.

Moravcová, L., Zákravský, P. & Hroudová, Z. 2001. Germination and seedling establishment in *Alisma gramineum*, *A. plantago-aquatica* and *A. lanceolatum* under different environmental conditions. *Folia Geobot.* 36: 131-146.

Müller-Schneider, P. 1986. Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Rübel Zür.* 85: 1-263.

Müller-Westermeier, G. 1990. *Klimadaten der Bundesrepublik Deutschland*. Deutscher Wetterdienst, Offenbach, DE.

Nicol, J.M., Ganf, G.G. & Pelton, G.A. 2003. Seedbanks of a southern Australian wetland: the influence of water regime on the final floristic composition. *Plant Ecol.* 168: 191-205.

Oberdorfer, E. 1983. *Pflanzensoziologische Exkursionsflora*, Ulmer, Stuttgart, DE.

Oberdorfer, E. 1992. *Süddeutsche Pflanzengesellschaften Teil I, Fels- und Mauergesellschaften, alpine Fluren, Wasser-, Verlandungs- und Moorgesellschaften.* Gustav Fischer Verlag, Jena, DE.

Oesau, A. & Froebe, H.A. 1972. Pflanzensoziologische Beobachtungen an hochwasserbeeinflussten Kulturflächen im nördlichen Oberrheintal. *Beiträge naturkundl. Forsch. SW-Deutschl.* 31: 65-86.

Oesau, A. 1972. Zur Soziologie von *Limosella aquatica* L. *Beiträge Biol. d. Pflanzen* 48: 377-397.

Oomes, M.J.M. & Elberse, W.T. 1976. Germination of six grassland herbs in microsites with different water contents. *J. Ecol.* 64: 745-755.

Oomes, M.J.M. 1990. Changes in dry matter and nutrient yields during the restoration of species-rich grasslands. *J. Veg. Sci.* 1: 333-338.

Oomes, M.J.M., Olff, H. & Altena, H.J. 1996. Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *J. Appl. Ecol.* 33: 576-588.

Oostermeijer, J.G.B., Van't Veer, R. & Den Nijs, J.C.M. 1994. Population-structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *J. Appl. Ecol.* 31: 428-438.

Otte, A. 1992. Entwicklung im Samenpotential von Ackerböden nach dem Aussetzen von Unkrautregulierungsmaßnahmen. *Landwirtschaftl. Jahrbuch* 69: 838-860.

Overbeck, G., Kiehl, K. & Abs, C. 2003. Seedling recruitment of *Succisella inflexa* in fen meadows: importance of seed and microsite availability. *Appl. Veg. Sci.* 6: 97-104.

Patzelt, A., Wild, U. & Pfadenhauer, J. 2001. Restoration of wet fen meadows by topsoil removal: Vegetation development and germination biology of fen species. *Restor. Ecol.* 9: 127-136.

Pfadenhauer, J. & Maas, D. 1987. Samenpotential in Niedermoorböden des Alpenvorlandes bei Grünlandnutzung unterschiedlicher Intensität. *Flora* 179: 85-97.

Poschlod, P., Bonn, S. & Bauer, U. 1996. *Ökologie und Management periodisch abgelassener und trocken fallender kleinerer Stehgewässer im oberschwäbischen und schwäbischen Voralpengebiet - Vegetationskundlicher Teil.* Landesanstalt für Umweltschutz Baden-Württemberg, Karlsruhe, DE.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *J. Appl. Ecol.* 39: 294-309.

Quinn, G.P. & Keough M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.

Riba, M., Picó, F.X. & Mayol, M. 2002. Effects of regional climate and small-scale habitat quality on performance in the relict species *Ramonda myconi*. *J. Veg. Sci.* 13: 259-268.

Roberts, H.A. 1981. Seedbanks in soil. *Adv. Appl. Biol.* 6: 1-55.

Roberts, H.A. & Neilson, J.E. 1981. Changes in the soil seedbank of four long-term crop/herbicide experiments. *J. Appl. Ecol.* 18: 661-668.

Römermann, C., Dutoit, T., Poschlod, P. & Buisson, E. 2005. Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. *Biol. Conserv.* 121: 21-33.

Rusch, G. & Fernandéz-Palacios, J.M. 1995. The influence of spatial heterogeneity on regeneration by seed in a Limestone Grassland. *J. Veg. Sci.* 6: 417-426.

Ryser, P. 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* 4: 195-202.

Scheiner, S.M. & Gurevitch, J. 1993. *Design and Analysis of Ecological Experiments*. Cambridge University Press, Cambridge,UK.

Schneider, R.L. & Sharitz, R.R. 1986. Seedbank dynamics in a southeastern riverine swamp. *Am. J. Bot.* 73: 1022-1030.

Schnittler, M. & Günther, K F. 1999. Central European vascular plants requiring priority conservation measures - an analysis from national Red Lists and distribution maps. *Biodivers. Cons.* 8: 891-925.

Seabloom, E.W., van der Valk, A.G. & Moloney, K.A. 1998. The role of water depth and soil temperature in determining initial composition of prairie wetland coenoclines. *Plant Ecol.* 138: 203-216.

Šeffer, J. & Stanová, V. 1999. *Morava River Floodplain Meadows - Importance, Restoration and Management.* DAPHNE - Centre for Applied Ecology, Bratislava, SK.

Silvertown, J.W. 1981. Micro-spatial heterogeneity and seedling demography in species-rich grassland. *New Phytol.* 88: 117-128.

Silvertown, J.W. & Dickie, J.B. 1981. Seedling survivorship in natural population of nine perennial chalk grassland plants. *New Phytol.* 88: 555-558.

Skoglund, J. 1990. Seedbanks, seed dispersal & regeneration processes in wetland areas. *Acta Universitatis Upsaliensis* 253: 1-33.

Skoglund, J. 1990. Seed dispersing agents in two regularly flooded river sites. *Can. J. Botany* 68: 754-760.

Smith, L.M. & Kadlec, J.A. 1983. Seedbanks and their role during drawdown of a North American marsh. *J. Appl. Ecol.* 20: 673-684.

Smith, R.S., Shiel, R.S., Millward, D., Corkhill, P. & Sanderson, R.A. 2002. Soil seed banks and the effects of meadow management on vegetation change in a 10-year meadow field trial. *J. Appl. Ecol.* 39: 279-293.

Špačková, I., Kotorová, I. & Lepš, J. 1998. Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotrophic wet meadow. *Folia Geobot.* 33: 17-30.

Stampfli, A. & Zeiter, M. 1999. Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. *J. Veg. Sci.* 10: 151-164.

Šumberová, K., Horáková, V. & Lososová, Z. In press. Vegetation dynamics on exposed pond bottoms in the Českobudějovická basin (South Bohemia). *Phytocoenologia.*

Tallowin, J., Kirkham, F., Smith, R. & Mountford, O. 1998. Residual effects of phosphorus fertilization on the restoration of floristic diversity to wet grassland. In: Joyce C.B. & Wade M.W. (eds.) *European Wet Grasslands,* pp. 249-275. Wiley, Chichester, UK.

Tallowin, J.R.B. & Smith, R.E.N. 2001. Restoration of a Cirsio-Molinietum fen meadow on an agriculturally improved pasture. *Restor. Ecol.* 9: 167-178.

Täuber, T. & Petersen, J. 2000. Isoëto-Nanojuncetea, In: Dierschke H. (ed.) *Synopsis der Pflanzengesellschaften Deutschlands.* Göttingen, DE.

Ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows - Software for Canonical Community Ordination (Version 4).* Centre for Biometry Wageningen, Wageningen, NL.

Ter Heerdt, G.N.J. & Drost, H.J. 1994. Potential for the development of marsh vegetation from the seedbank after a drawdown. *Biol. Conserv.* 67: 1-11.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. 1996. An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. *Funct. Ecol.* 10: 144-151.

Ter Heerdt, G.N.J., Schutter, A. & Bakker, J.P. 1999. The effect of water supply on seedbank analysis using the seedling-emergence method. *Funct. Ecol.* 13: 428-430.

Thomas, P. 1990. Grünlandgesellschaften und Grünlandbrachen in der nordbadischen Rheinaue. *Diss. Bot.* 110: 1-234.

Thompson, K. & Grime, J.P. 1979. Seasonal variation in the seedbanks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67: 893-921.

Thompson, K., Band, S.R. & Hodgson, J.G. 1993. Seed size and shape predict persistence in soil. *Funct. Ecol.* 7: 236-241.

Thompson, K., Bakker, J.P. & Bekker, R.M. 1997. *The soil seed banks of North West Europe: methodology, density and longevity.* Cambridge University Press, Cambridge, UK.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.

Tockner, K., Malard, F. & Ward, J.V. 2000. An extension of the flood pulse concept. *Hydrol. Process.* 14: 2861-2883.

van den Brink, F.W.B., van der Velde, G., Bosman, W.W. & Coops, H. 1995. Effects of substrate parameters on growth-responses of 8 helophyte species in relation to flooding. *Aquat. Bot.* 50: 79-97.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114.

van der Sman, A.J.M., Joosten, N.N. & Blom, C.W.P.M. 1993. Flooding regimes and life-history characteristics of short-lived species in river forelands. *J. Ecol.* 81: 121-130.

van der Toorn, J. 1980. On the ecology of *Cotula coronopifolia* and *Ranunculus sceleratus* L. - Geographical distribution, habitat and field observations. *Acta Bot. Neerl.* 29: 385-396.

van der Valk, A.G. & Davis, C.B. 1978. The role of seedbanks in the vegetation dynamics of prairie glacial marshes. *Ecology* 59: 322-335.

van Duren, I.C., Strykstra, R.J., Grootjans, A.P., ter Heerdt, G.N.J. & Pegtel, D.M. 1998. A multidisciplinary evaluation of restoration measures in a degraded Cirsio-Molinietum fen meadow. *Appl. Veg. Sci.* 1: 115-130.

van Tooren, B.F. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. *Oikos* 53: 41-48.

Vécrin, M.P., van Diggelen, R., Grévilliot, F. & Muller, S. 2002. Restoration of species-rich flood-plain meadows from abandoned arable fields in NE France. *Appl. Veg. Sci*. 5: 263-270.

Venterink, H.O., Wassen, M.J., Belgers, J.D.M. & Verhoeven, J.T.A. 2001. Control of environmental variables on species density in fens and meadows: importance of direct effects and effects through community biomass. *J. Ecol.* 89: 1033-1040.

Verhagen, R., Klooker, J., Bakker, J.P. & van Diggelen, R. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Appl. Veg. Sci.* 4: 75-82.

Vogt, K., Rasran, L. & Jensen, K. 2004. Water-borne seed transport and seed deposition during flooding in a small river-valley in Northern Germany. *Flora* 199: 377-388.

Waldhardt, R., Fuhr-Boßdorf, K. & Otte, A. 2001. The significance of the seed bank as a potential for the reestablishment of arable-land vegetation in a marginal cultivated landscape. *Web Ecology* 2: 83-87.

Walker, K.J., Stevens, P.A., Stevens D.P., Mountford J.O., Manchester S.J. & Pywell R.F. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biol. Conserv*. 119: 1-18.

Wassen, M.J., Peeters, W.H.M. & Venterink, H.O. 2003. Patterns in vegetation, hydrology, and nutrient availability in an undisturbed river floodplain in Poland. *Plant Ecol.* 165: 27-43.

Watkinson, A.R. & Powell, J.C. 1993. Seedling recruitment and the maintenance of clonal diversity in plant populations - a computer simulation of *Ranunculus repens*. *J. Ecol.* 81: 707-717.

Watt, T.A. & Gibson, C.W.D. 1988. The effects of sheep grazing on seedling establishment and survival in grassland. *Vegetatio* 78: 91-98.

Welk, E. 2002. Arealkundliche Analyse und Bewertung der Schutzrelevanz seltener Gefäßpflanzen Deutschlands. *Schriftenr. Vegetationsk.* 37: 1-337.

Wisskirchen, R. & Haeupler, H. 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands.* Ulmer, Stuttgart, DE.

Zahlheimer, W.A. 1979. Vegetationsstudien in den Donauauen zwischen Regensburg und Straubing als Grundlage für den Naturschutz. *Hoppea* 38: 3-398.

Zar, J.H. 1999. *Biostatistical Analysis.* Prentice-Hall, Upper Saddle River, NJ, US.

Dank

Für die Anleitung der Dissertation und die vielfältige Unterstützung während der Arbeit möchte ich Frau Prof. Dr. Dr. A. Otte herzlich danken. Herrn Prof. Dr. G. Esser danke ich für die Übernahme des Korreferats.

Ein besonderer Dank für die sehr gute und erfolgreiche Zusammenarbeit gilt dem „Stromtalwiesen-Team“. Dr. Norbert Hölzel danke ich für die sehr engagierte Betreuung, zahlreiche Anregungen und die unermüdliche, kritische Durchsicht der Manuskripte. Tobias Donath möchte ich für das geduldige Antworten auf viele Fragen, gute Ratschläge zur Statistik und das gemeinsame Durchstehen von einigen sehr heißen, mückenreichen Geländetagen danken. Auch Matthias Harnisch, der das E+E –Vorhaben „Stromtalwiesen“ vor Ort in Riedstadt koordiniert, sei gedankt.

Für das Interesse am E+E-Vorhabens „Stromtalwiesen“ danke ich Frau Gollub, Herrn Bohn und Herrn Fechtel aus dem Bundesamt für Naturschutz (BfN), das die Finanzierung bereitgestellt hat.

Christiane Lenz-Kuhl und Josef Scholz vom Hofe haben durch tatkräftige und sehr geduldige Unterstützung beim Keimlinge zupfen, Biomasse ernten, mähen der Versuchsflächen u.v.m. zum Gelingen der Arbeit beigetragen.

Für das Korrekturlesen der Manuskripte und der Dissertation sowie für die vielen Anregungen und die konstruktiven Kommentare zu den Untersuchungen danke ich Dr. Lutz Eckstein.

Bei allen Mitarbeitern der Professur für Landschaftsökologie möchte ich mich für die gute und freundliche Arbeitsatmosphäre, viele interessante Diskussionen und für die netten Kaffeepausen mit viel Schokolade und Keksen bedanken. Insbesondere Birgit Reger danke ich für ihre große Hilfsbereitschaft.

Zum Schluss möchte ich meiner Familie und Jens für die uneingeschränkte Unterstützung und Ermutigung während der ganzen Promotionszeit danken.